

TABLE 2. Pollen-Size in Engelhardia

SPECIES	DATA FROM PRESENT STUDY *		STACHURSKA (1961)
	\bar{X} (μ)	RANGE (μ)	RANGE (μ)
§ ENGELHARDIA			
<i>E. apoensis</i> ***	17.8	15.1–20.3	
<i>E. nudiflora</i>	18.9	16.8–20.8	
<i>E. parvifolia</i> **	20.3	17.2–23.0	19.6–24.9
<i>E. serrata</i>			
var. <i>cambodica</i>	20.9	18.9–23.8	
<i>E. spicata</i>			19.6–24.9
var. (?) ***	21.9	19.2–24.0	15.7–22.7
<i>E. spicata</i>			
var. <i>acerifolia</i> ***	19.6	16.8–20.8	19.2–24.5
<i>E. spicata</i>			
var. <i>colebrookiana</i> **	22.0	20.0–24.8	21.0–31.5
§ PSILOCARPEAE			
<i>E. roxburghiana</i>	14.8 †	12.8–17.4 †	14.2–17.3
§ OREOMUNNEA			
<i>E. pterocarpa</i>	20.5	18.0–23.2	

* n = 50 for each collection

** forms with irregularly thickened exine occasional

*** forms with irregularly thickened exine predominant

† average of three collections

surfaces. This would suggest that the feature is due to an uneven thickening of the columella layer. Since the scabrate sculpture is present even on the concavities it is apparent that at least some tectum is present.

Individual grains of *Engelhardia* vary in size from 12.8 micra (*E. chrysolepis*, $\bar{X} = 14.8\mu$) to 24.8 μ (*E. spicata* var. *colebrookiana*, $\bar{X} = 22.0\mu$) (TABLE 2). The exine is generally relatively uniform in thickness (ca. one micron) over the entire grain surface (except as noted above). The scabrate sculpture, consisting of evenly spaced elements less than 0.4 micra in diameter, is also present over the whole surface of the grain. It is most distinct in grains of *E. nudiflora* and *E. pterocarpa* and least so in *E. chrysolepis*.

Interspecific pollen morphological differences are evident in the genus, although a greater range of material must be studied before definite conclusions can be made. Tentatively it can be suggested that there are three basic pollen types within the genus. These can be designated arbitrarily as *E. chrysolepis* type, *E. nudiflora-Aljaroa* type, and *E. spicata* type.

Grains of the *Engelhardia chrysolepis* type are distinct. The grains are extremely small (12.8–17.4 μ), distinctly triangular in polar view, oblate (index 0.57), endopore is elongated equatorially, exopore is elongated meridionally, ectexine does not thicken at the pore, no columellae are discernible, and the scabrate sculpture is extremely fine. On the basis of

the material studied, this type occurs only in *E. chrysolepis*. This is consistent with the findings of Stachurska (1961).

Pollen grains of the *E. nudiflora-Alfaroa* type are larger (16.8–23.8 μ), rounded-triangular in polar view, suboblate (index 0.76), endopore is not elongated equatorially, exopore is more or less circular, ektexine thickens slightly within the vestibulum, columellae are visible within the vestibulum, and the sculptural pattern is more distinct. This type has been found in *E. nudiflora*, *E. pterocarpa*, and *E. serrata* var. *cambodica*. This pollen type is similar in most respects to *Alfaroa*.

The *Engelhardia spicata* type is similar to the *E. nudiflora-Alfaroa* type, but differs in that the grains are apt to be oblate-spheroidal (index 0.89) and possess the variable differentially thickened exine. This makes the grains angular in polar view (Stachurska refers to these as "hexagonal forms"). As mentioned previously, the angularity is due to a sharply undulating exine, possibly a function of uneven thickening. Along the ridges (thickened areas) columellae can sometimes be seen. In many grains of the *E. spicata* type the vestibulum is not clearly developed. The fact that not all of the grains of a sample possess the differential thickening and that the degree of expression is variable renders an interpretation difficult. The morphological and taxonomic significance of the feature can be assessed more properly through the study of thin sections.

In the present study grains of the *E. spicata* type were found strongly developed in collections of *E. spicata*, *E. spicata* var. *acerifolia*, and *E. apoensis*, and less frequently developed in collections of *E. parvifolia* and *E. spicata* var. *colebrookiana*. Stachurska has reported it in *E. parvifolia*, *E. spicata*, and *E. philippinensis* (= *E. spicata*) and to a lesser degree in *E. colebrookiana* (= *E. spicata* var. *colebrookiana*) and *E. acerifolia* (= *E. spicata* var. *acerifolia*).

Platycarya

The pollen grains of *Platycarya* are tectate, triporate (2–5 pores), oblate in shape, triangular in polar view, and possess a fine scabrate sculpture (TEXT-FIGURES 16–24). The grains are unique in possessing a pair of arcuate pseudocolpi on each polar hemisphere. The pores are equatorial in position, the endopore is elongated equatorially, and the exopore meridionally (TEXT-FIGURE 23).

The pseudocolpi are distinctive features. They are sharp, slit-like thinning of the ektexine, involving either the inner portion of the tectum or deeper layers of the ektexine. The outer layer of the tectum, although sharply invaginated, is continuous over the pseudocolpi, since the scabrate sculpture is visible in these regions. The longer of the two pseudocolpi on each hemisphere describes an arc of about 12 micra, the shorter one of approximately six micra. The functional significance of the structures is not known, but their similarity to colpi led Faegri and Iversen (1950) to classify the grains as extraporate (possessing both pores and colpi but with the pores not included in the colpi).

The exine is essentially homogeneous and of uniform thickness. Colu-

mellae cannot be differentiated. The scabrate sculpture is present over the whole surface, including vestibulum and pseudocolpi, and consists of evenly spaced elements (micro-echinae?) less than 0.3 micra in diameter.

The grains of *Platycarya* vary in size from 13.1 to 17.2 micra (mean about 15.0 μ) (See TABLE 3).

TABLE 3. Pollen-Size in *Platycarya strobilacea*

DATA FROM PRESENT STUDY *		DATA FROM STACHURSKA (1961)
\bar{X} (μ)	RANGE (μ)	RANGE (μ)
14.5	13.1-15.6	18.7-22.0 **
15.5	13.1-17.2	22.0-27.0 ***
Ave: 15.0	13.1-17.2	24.0-27.0 †

* n = 50 for each collection

** triporate grains

*** tetraporate grains

† pentaporate grains

It is interesting to note that, aside from the presence of pseudocolpi, the grains of *Platycarya* are remarkably similar to those of the *Engelhardia chrysolepis* type; both are small, triangular, oblate, possess an elongated vestibulum and pore aperture, an essentially homogeneous exine, and a fine scabrate sculpture.

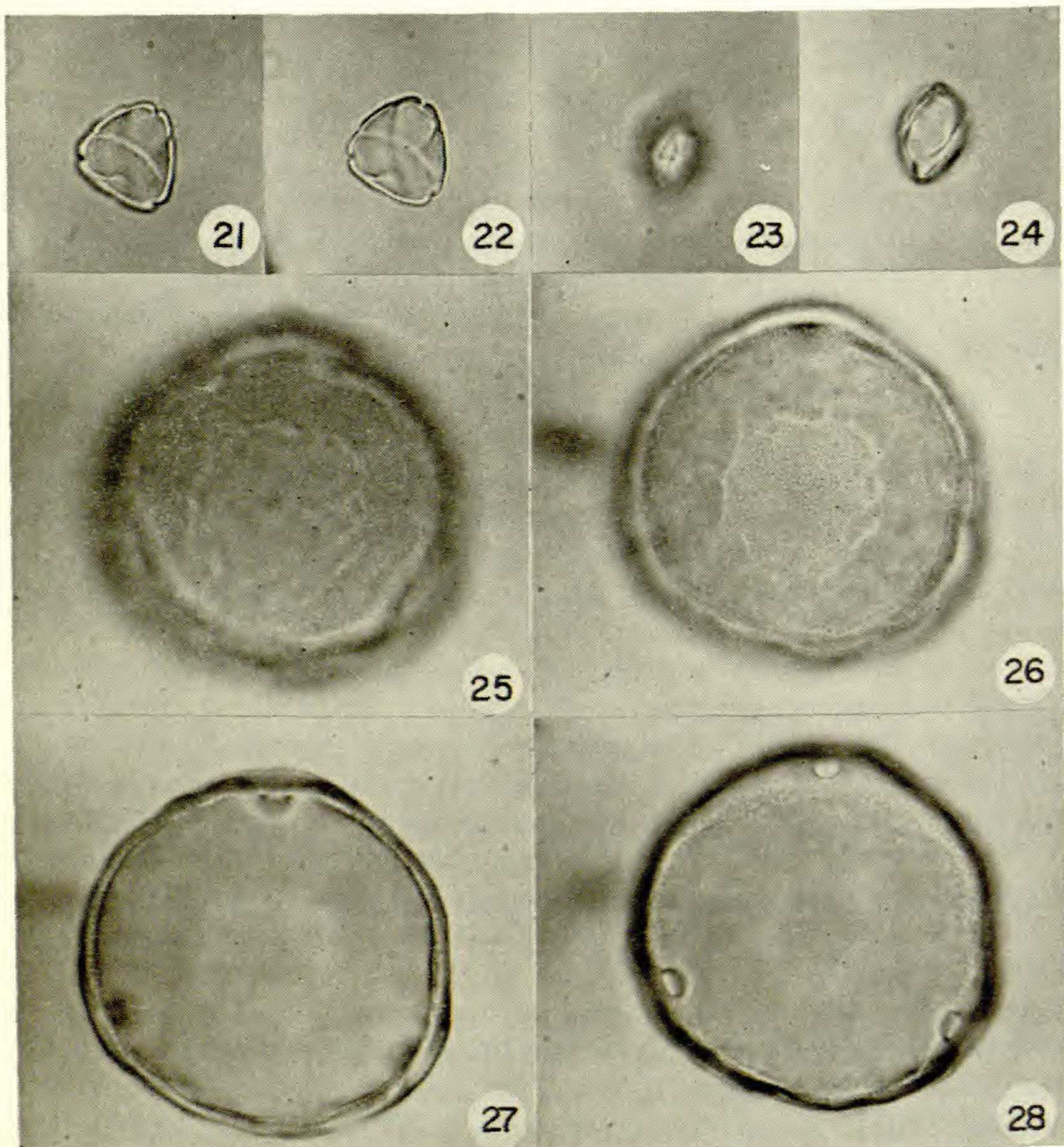
Carya

The pollen grains of *Carya* are tectate, triporate (1-6 pores have been observed), suboblate in shape, rounded-triangular to circular in polar view, and possess a fine scabrate sculpture (TEXT-FIGURES 25-49, 101-104). The grains are distinctly heteropolar; the pores are never exactly equatorial in position, but drawn somewhat towards one pole (the distal), leaving one hemisphere (proximal) pore-free. Correlated with the heteropolarity is a distinct thinning of the exine on the proximal pole (TEXT-FIGURES 25, 26, 33-36). The pore vestibulum is an open, low to greatly flattened cone. It is delimited by the endexine which stops approximately four to six micra short of the exopore, leaving a low, poorly defined rim (TEXT-FIGURES 31, 32, 37). The ektexine thickens quite distinctly within the vestibulum; the pore aperture is more or less circular in outline.

The pollen grains of *Carya* vary in size from 26.5 μ (one grain of *Carya cordiformis*) to 63.2 μ (one grain of *C. tomentosa*). Mean pollen size ranges from 33.3 μ for *C. tonkinensis* (one collection) to 50.7 μ for *C. tomentosa* (11 collections). TABLE 4 summarizes these data and those of Stone (1963), Andersen and Cain (personal communication), and Stachurska (1961). In general, grains seem to be largest in section CARYA and smallest in section APOCARYA. More important, however, is the correlation between ploidal level and grain size (Stone 1961, 1963; Whitehead, 1963). The tetraploids of section CARYA possess the largest grains.

The ektexine of *Carya* grains is distinctly stratified. This is especially evident within the vestibulum, where a distinct thick tectum is present, in addition to a well developed columella layer. The endexine, not present within the vestibulum, is relatively thin. Work with electron microscopy (Stone *et al.*, 1964) indicates that the layer identified as endexine with light and phase microscopy actually consists of the innermost layer of ektexine (foot layer) and endexine.

The ektexinous thickening near the pore involves two layers of which the columella layer is the primary contributor. In most species of *Carya* the columellae can only be seen within the area of the ektexinous thickening (which may coincide in extent with the vestibulum or stretch slightly beyond it). In general the columellae in this region are highly variable in



TEXT-FIGURES 21-28. Magnification 690 \times . Each series (e.g., 25-28) represents successively lower levels of focus. 21-24, *Platycarya strobilacea*, polar view (21, 22, continuation of series beginning at 16); equatorial view (23, 24). 25-28, *Carya tomentosa*, polar view.

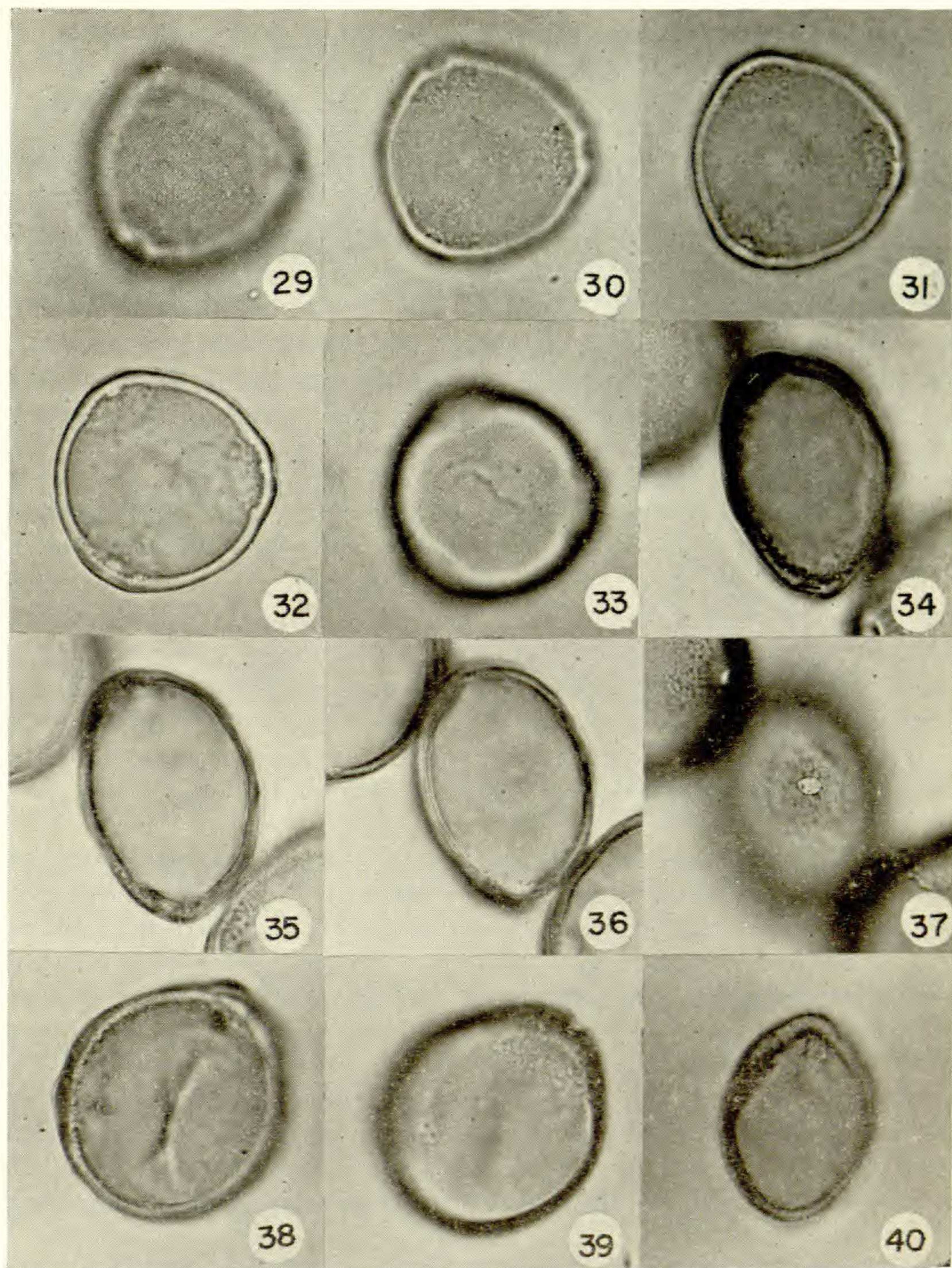
TABLE 4. *Carya* Pollen-Size Data

		WHITEHEAD			STONE			ANDERSEN & CAIN			STACHURSKA	
		\bar{X}	RANGE OF VARIATION	No. COLL.	\bar{X}	RANGE OF VARIATION	No. COLL.	\bar{X}	RANGE OF VARIATION	No. COLL.	RANGE OF VARIATION	"MOST FREQUENT DIAMETER"
§ <i>CARYA</i>												
<i>carolinae-septentrionalis</i>	(2n)	—	— —	—	43.7	42-45	3	—	—	—	—	—
<i>floridana</i>	(4n)	—	— —	—	44.1	41-47	7	—	—	—	—	—
<i>glabra</i>	(4n)	46.88	40.80-53.04	2	51.7	48-57	11	50.37	43-47	5	38.5-59.5	49.0-52.5
<i>laciniosa</i>	(2n)	45.00	38.76-51.00	2	47.5	46-50	6	46.82	41-53	5	45.5-48.2	52.5-54.2
<i>leiodermis</i>		47.49	40.80-53.04	1	49.7	46-54	7	—	—	—	—	—
<i>ovalis</i>	(4n)	47.65	36.72-53.04	2	50.4	48-53	11	52.81	46-59	4	56.0-96.5	65.5
<i>ovata</i>	(2n)	44.93	36.72-51.00	3	46.5	43-52	13	48.30	42-54	5	42.0-61.2	49.0-52.5
<i>pallida</i>		49.82	42.84-55.08	1	49.3	45-54	7	—	—	—	53.0-75.0	62.0
<i>texana</i>	(4n)	46.27	40.80-53.04	2	48.2	42-52	16	—	—	—	—	—
<i>tomentosa</i>	(4n)	50.65	40.80-63.24	11	51.9	49-57	22	52.53	47-60	5	45.5-59.5	52.5
<i>glabra</i> (Florida)		—	— —	—	47.7	44-50	15	—	—	—	—	—
§ <i>APOCARYA</i>												
<i>aquatica</i>	(2n)	41.80	36.72-46.92	2	41.7	40-46	4	—	—	—	36.4-54.2	43.7
<i>cathayensis</i>		—	— —	—	—	—	—	—	—	—	—	—
<i>cordiformis</i>	(2n)	40.36	26.52-46.92	11	42.0	40-44	11	42.61	39-48	5	40.2-50.7	45.5-47.2
<i>illinoensis</i>	(2n)	46.10	38.76-55.08	2	48.0	43-53	9	—	—	—	38.5-56.0	49.0
<i>myristiciformis</i>	(2n)	39.64	32.64-44.88	2	42.1	39-47	15	—	—	—	38.5-52.5	43.7-52.5
<i>tonkinensis</i>		33.25	28.56-38.76	1	32.6	32-33	3	—	—	—	—	—
<i>poilanei</i>		—	— —	—	38.5	—	1	—	—	—	—	—
<i>palmeri</i>		—	— —	—	44.4	42-46	14	—	—	—	—	—
× <i>lecontei</i>		—	— —	—	47.9	47-49	2	—	—	—	—	—
§ <i>RHAMPHOCARYA</i>												
<i>sinensis</i>		38.23	30.60-44.88	1	35.7	—	1	—	—	—	—	—

size and are irregularly distributed (TEXT-FIGURES 101–104). Clumping of columellae is not infrequent. In only a few species can columellae be differentiated in the polar region (and never on the proximal pole), and there they are invariably smaller and more tightly packed. There is usually a rather uniform gradation from pole to pore, with columellae becoming progressively larger and more widely spaced. In some species (e.g., *C. tonkinensis*, TEXT-FIGURE 102) there is a sharp line of demarcation between polar region and vestibulum. In those species in which the columellae are most distinct, there is also a gradient between pole and interporium (equatorial region between the pores). The columellae are visible in the interporium, but smaller and more tightly packed than in the vestibulum. As can be seen in the electron micrographs of Stone *et al.* (1964), a columella layer is actually present in all portions of the grain; columellae, appearing as “variable-sized, anastomosing rods,” can be differentiated throughout. The distribution detected with light and phase microscopy is therefore partly an artifact caused by limitations of technique. Too few data are available as yet to indicate whether columella distribution can be used to characterize species, although some possibilities appear to be present. These are noted at the end of this section and in the discussion.

The thin polar area poses some problems of interpretation. If one follows Stachurska (1961) and Wodehouse (1935), it is not a question of a thinning of the exine, but of the exinous thickenings which surround the pores coalescing and leaving only the pole free. However, by careful observation with light and phase microscopy (oil immersion) it is possible to determine the extent of the ektexinous thickening; i.e., the region within which the columellae can be differentiated most readily and within which they have the most irregular distribution. In those species which possess the most extensive ektexinous thickening (continuing beyond the vestibulum and encroaching upon distal pole and interporium, e.g., *Carya cordiformis*, TEXT-FIGURE 103), the interpretation of Stachurska and Wodehouse would seem to fit. However, even in such types it can be seen that the polar thinning is considerably more restricted in area than the region covered by the ektexinous thickening. Furthermore, in *Carya tonkinensis* (TEXT-FIGURE 102) the thickenings are confined to the vestibulum (which itself is highly restricted), yet a distinct polar thinning is visible (TEXT-FIGURE 33). It would thus seem that the polar thinning is a feature unrelated to the exinous thickenings surrounding the pores. The thinning probably involves largely the columella layer as columellae are never visible in this region, and since the scabrate sculpture is continuous over the thinning. This interpretation has been corroborated by electron microscopy (Stone *et al.*, 1964).

As suggested above, it is extremely difficult to attach any taxonomic significance to the morphological features observed. There is great variation from collection to collection and occasionally within a collection as well. This is true with respect to the frequency of tetraporate grains, columella distribution, character of the ektexinous thickening, degree of



TEXT-FIGURES 29-40. Magnification $690\times$. Each series (e.g., 29-33) represents successively lower levels of focus. 29-33, *Carya tonkinensis*, polar view. 34-40, *Carya aquatica*, 34-37, equatorial view to show polar thinning; 38, 39, diporate grain; 40, monoporate grain.

heteropolarity, etc. Stachurska's pollen groups seem to be more a reflection of the particular grains studied than characteristic of the species in question. This is certainly true with respect to pore frequency, extent of the exinous thickening, and position of the pores. The author found no grains with truly equatorial pores in any of the collections studied, al-

though less heteropolar grains were found in a few species (e.g., *C. tonkinensis*, *C. sinensis*, *C. illinoensis*, etc.).

The observations on fine structure made in the course of the investigation are summarized in the following paragraphs.

Section CARYA. (1) *Carya glabra* (2 collections): columellae within vestibulum large and distinct, irregular in size and distribution. Columellae visible on distal pole are small and tightly packed. Uniform gradation from pole to both pore and interporium. Columellae visible in interporium, but very tightly packed. (2) *C. laciniosa* (2 collections): arrangement of columellae as for *C. glabra*. (3) *C. leiodermis* (1 collection): morphology as for two preceding species, but structure finer, columellae not discernible on pole and interporium. (4) *C. ovalis* (2 collections): structure intermediate between *C. glabra* and *C. leiodermis*. Some columellae visible on distal pole, but very fine and tightly packed. (5) *C. ovata* (3 collections): much variation from collection to collection; one similar to preceding species, with very fine columellae visible on interporium; another with extremely coarse and widely spaced columellae within vestibulum and distinct large columellae on the distal pole; a third with an extraordinarily thick tectum and columella layer within the vestibulum. (6) *C. pallida* (1 collection): ektexine within the vestibulum unusually thick (reported also by Stachurska), exine varies in thickness over the surface of the grain giving a rather undulating appearance. Columella distribution as in grains of *C. glabra*. (7) *C. texana* var. *arkansana* (2 collections): grains more regular than in the preceding species, outline regularly rounded-triangular. Vestibulum sharply defined. Abrupt transition from vestibulum to polar area. Very large and irregularly distributed columellae within vestibulum; columellae not visible on rest of grain surface. (8) *C. tomentosa* (11 collections): In general, columellae visible on both interporium and distal pole, with a gradation from both pole and interporium to vestibulum (and from pole to interporium) (TEXT-FIGURE 104). Packing of columellae is variable.

Section APOCARYA. (1) *C. aquatica* (2 collections): collections variable, one with uniform gradation from pole to pore zone and with columellae relatively tightly packed within pore zone and not visible on the pole; the other with a sharp line of demarcation between polar zone and pore zone, and columellae within pore zone very large and widely spaced. (2) *C. cordiformis* (11 collections): Much variability is evident. In general, the ektexinous thickenings are extensive and encroach upon both interporium and distal pole (TEXT-FIGURE 103). The columellae within the ektexinous thickenings are usually large and irregularly spaced. Some collections have an unusually wide spacing of columellae, giving the vestibulum an essentially "empty" look (TEXT-FIGURE 103). In some collections there is a gradation from pole to pore, in others an abrupt change (the latter condition seems to prevail in two collections of *C. cordiformis* var. *latifolia*). (3) *C. illinoensis* (2 collections): the pollen grains appear to be more triangular than in many of the preceding species, apparently due to a distinct, localized thickening of the ektexine at the pore. The grains

also tend to be a little less heteropolar. Both the vestibulum and ektexinous thickening are restricted in area and there is a sharp contrast in columella pattern between this region and the polar hemispheres. Within the pore zone the columellae are highly irregular in size and shape. The relatively small area covered by the ektexinous thickening corresponds to the reports of Wodehouse (1935) and Stachurska (1961). (4) *C. myristiciformis* (2 collections): columella distribution gradational from pole to pore, columellae not visible on pole. A few "islands" of tightly packed fine columellae are evident on the distal pole of a few grains from one collection. The columellae within the vestibulum are more uniformly distributed and more tightly packed than in most species. (5) *C. tonkinensis* (1 collection): pollen grains are very small; pores more equatorial than in other species; endexine break at border of vestibulum more distinct than in most; vestibulum and ektexinous thickening very restricted. Columellae visible only within the vestibular area. Columellae large, irregular, and widely spaced (TEXT-FIGURE 102). Sharp lines of demarcation between vestibulum and polar zone (partly due to break in endexine, partly to the change in columella distribution). There is an apparent concentration of columellae at the base of the vestibulum (near the endexine break) and also around the aperture.

Section RHAMPHOCARYA. (1) *Carya sinensis* (1 collection): grains relatively small (see also Stone, 1963), somewhat more triangular in polar view than other species, and a little less heteropolar. Vestibulum restricted as in *C. tonkinensis*, and defined by a rather sharp break of the endexine. Ektexinous thickening restricted in area, sharp line of demarcation between pore area (within which are large, irregular, widely spaced columellae) and polar hemispheres (TEXT-FIGURE 101). Thinning of proximal pole as in all other species.

On the basis of size, restricted ektexinous thickening, slightly protuberant pores, and relative isopolarity, grains of *Carya tonkinensis* and *C. sinensis* approach those of the *Engelhardia nudiflora-Aljaroa* type. This might indicate that grains of these species are primitive for the genus. Should this assumption be valid, then one may suggest that the evolutionary trends within the genus (with respect to pollen morphology) would be towards increased pollen size, increased heteropolarity, more extensive ektexinous thickenings and the development of larger and more distinctive columellae. Pollen size and heteropolarity are to a degree related, and the ektexinous thickenings and columella patterns are certainly related. However, the former two and latter two could be thought of as relatively independent evolutionary trends.

The grains of *Carya sinensis* are worthy of further comment, especially considering the varied opinions held concerning the taxonomic position of the species (e.g., Manning and Hjelmqvist, 1951; Scott, 1953; and Leroy, 1952, 1953). On the basis of pollen morphology alone, the taxon would appear to be closely allied to *Carya*. The grains are clearly *Carya*-like; in fact, indistinguishable from those of many of the species. This would certainly support the conclusions of Manning and Hjelmqvist (loc. cit.) who

have placed it in section RHAMPHOCARYA of the genus *Carya*. As was suggested to the writer by Stone (personal communication) the greater degree of triangularity of *Carya sinensis* grains (compared to *C. tonkinensis*), a condition noted in grains of the *Alfaroa-Engelhardia nudiflora* type, indicates that the *sinensis* type might be more primitive than the *tonkinensis* type.

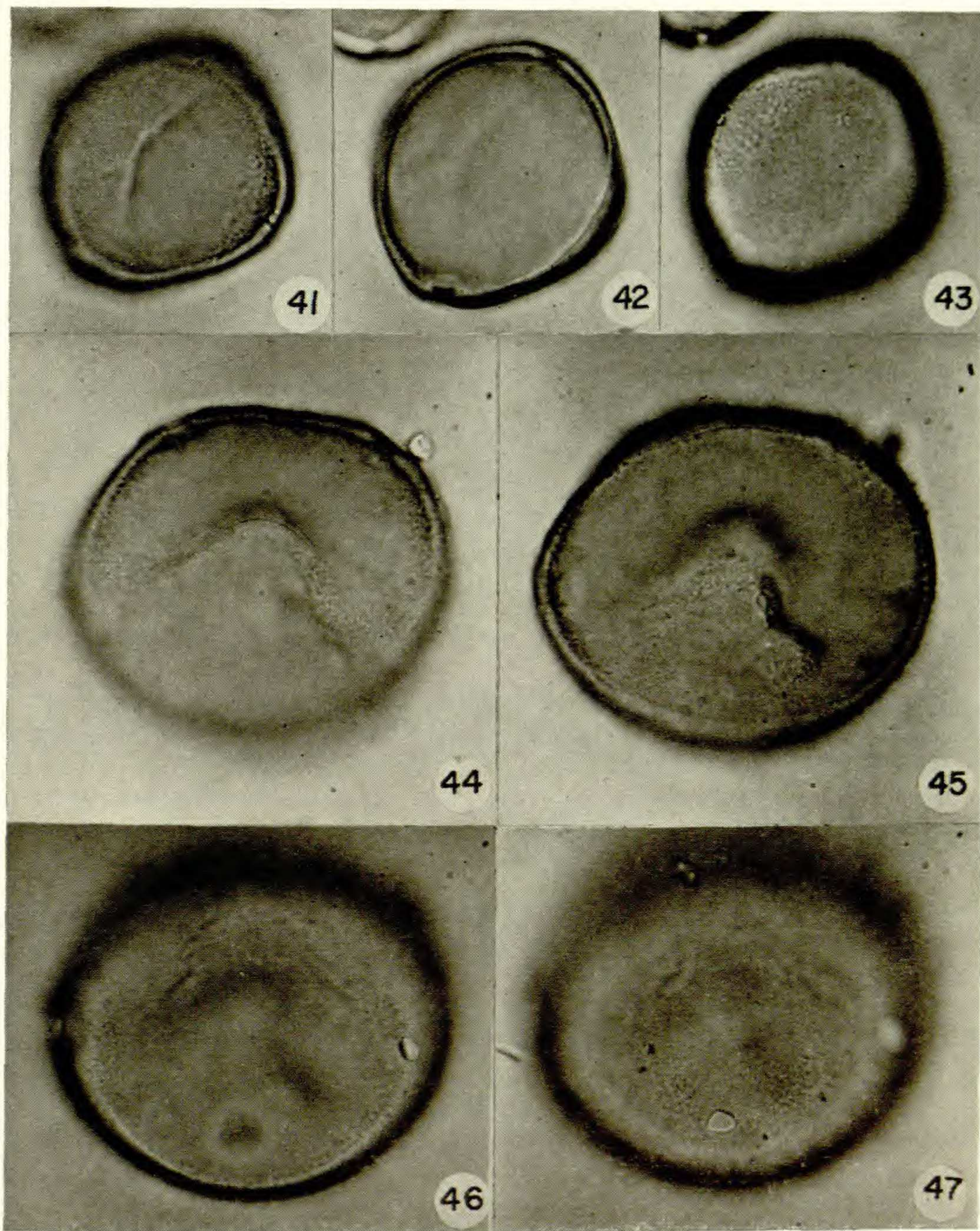
Pterocarya

The pollen grains of *Pterocarya* are prevaillingly stephanoporate, possess from three to nine pores (the mean figure is roughly 5.8 for the genus), are polygonal to circular in polar view, oblate to suboblate in shape, and have a distinct scabrate sculpture (TEXT-FIGURES 80–100, 106). The pores are distinctly aspidate, the ektexine generally thickens perceptibly within the vestibulum, and the pore aperture varies in shape from circular (TEXT-FIGURE 92) to elongate (TEXT-FIGURE 91). Elongate apertures tend to be more frequent than circular ones. The grains, although characteristically stephanoporate, are occasionally periporate and heteropolar as in *Juglans* (TEXT-FIGURES 92–94). This condition is most prevalent in grains with seven or more pores. The heteropolar grains generally possess only one or two pores on the distal surface, the remaining pores being strictly equatorial in position. The frequency of heteropolar grains varies from collection to collection. It is lowest in one collection of *Pterocarya paliurus* (0%) and highest in a collection of *Pt. rhoifolia* (34%) (see TABLE 5). Some tendency towards heteropolarity can be found in many other stephanoporate grains in that one or two pores may be positioned slightly off of the equator, and the grains are often slightly plano-convex in equatorial view. No evidence of any ektexinous thinning on the proximal side has been found.

Grains of *Pterocarya* vary in size from 25.9μ (one grain of *Pt. paliurus*) to 38.8μ (several species). Mean pollen size varies from 28.6μ (*Pt. hupehensis*, 1 collection) to 35.5μ (*Pt. insignis*, 1 collection). Pore number varies from 3 to 9. Species' means range from 4.1 (*Pt. paliurus*) to 6.5 (*Pt. rhoifolia*). (For the purpose of these discussions, Stachurska's observations on *Pt. rhoifolia* have been omitted. The collection that she studied had unusually high pore number for the genus (7.6), an unusually high percentage of heteropolar grains (75%), and the modal class for pollen size was larger than for other species of *Pterocarya*. It is likely that this herbarium sheet was identified incorrectly and represents instead a species of *Juglans* (possibly *J. cathayensis*.)

The individual collection data for mean pore number and mean pollen size are plotted on a scatter diagram (FIGURE 108).

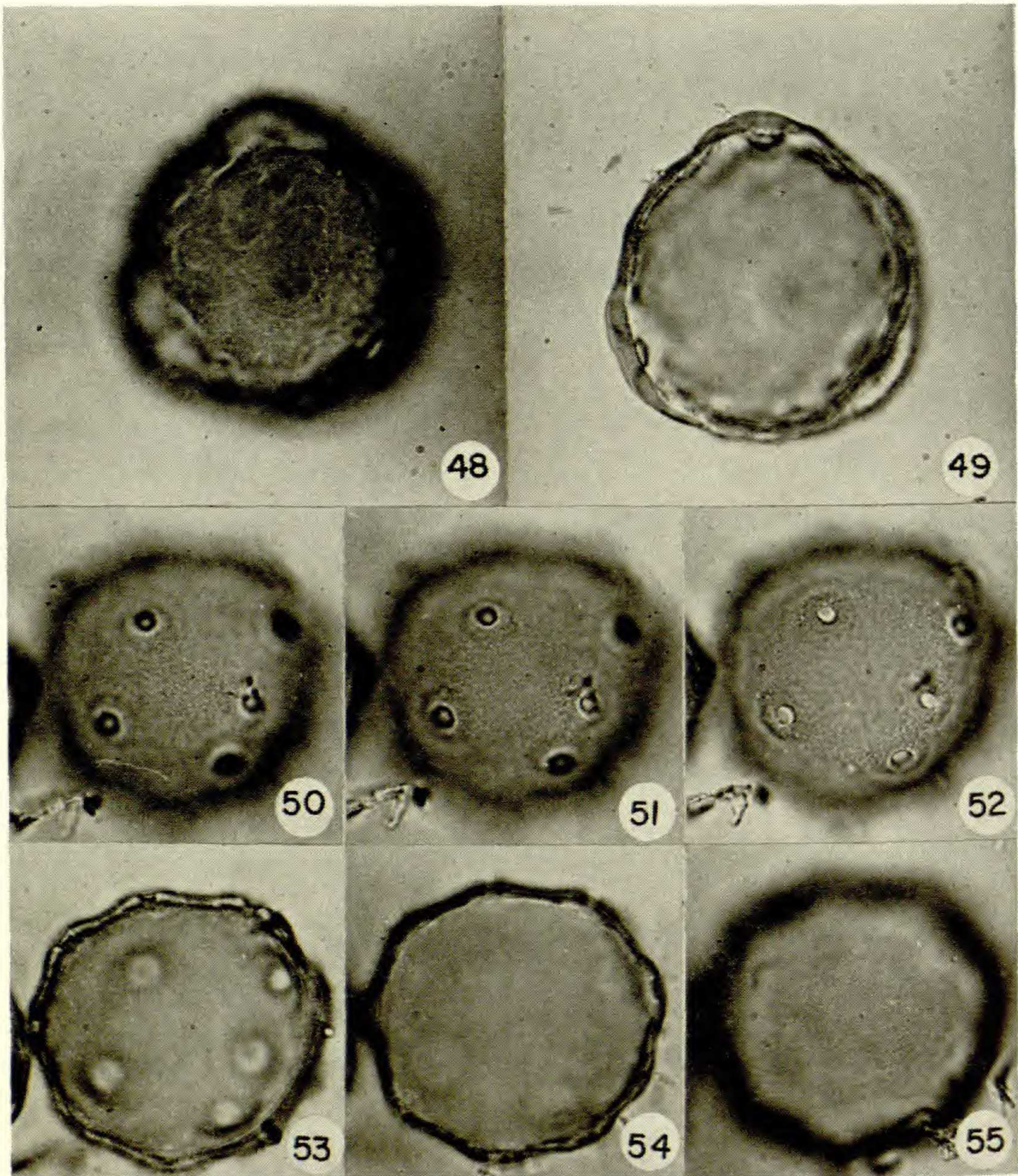
The exine of *Pterocarya* grains is relatively homogeneous. Columellae can never be distinguished outside of the vestibular region and are often difficult to discern even within that zone. The ektexine thickens very slightly at the pore. Both tectum and columella layer are involved in this thickening. The vestibulum of the pore is a relatively distinct feature,



TEXT-FIGURES 41-47. Magnification $690\times$. Each series (e.g., 41-43) represents successively lower levels of focus. 41-43, *Carya aquatica*, polar view, tetraporate grain. 44-47, *Carya glabra*, polar view, hexaporate grain.

partly because the endexine breaks off sharply at the base of the vestibulum and partly because there is a concentration of columellae at that point and around the aperture. The remainder of the ectexine within the vestibulum is often free of columellae.

With the exception of low pore number in *Pterocarya paliurus* (section CYCLOPTERA) there appear to be no morphological criteria which have any intrageneric taxonomic significance.



TEXT-FIGURES 48-55. Magnification $690\times$. Each series (e.g., 50-55) represents successively lower levels of focus. 48, 49, *Carya pallida*, polar view. 50-55, *Juglans regia*, polar view.

Juglans

The pollen grains of *Juglans* are relatively variable. They (TEXT-FIGURES 50-79, 107) are tectate and basically periporate and heteropolar. The pores are restricted to one polar hemisphere or may encroach slightly upon the other. Pore number varies from two to 37 for the genus, although individuals with from 6 to 18 pores are most frequent. The mean pore-number varies from a minimum of 7.3 for *J. cathayensis* (2 collections) to a maximum of 17.4 for *J. nigra* (42 collections; Whitehead, 1963). The pores are apt to be strictly equatorial in grains with low pore number, hence such grains can be classified as stephanoporate (TEXT-

TABLE 5. Pollen-Size and Pore-Number in *Pterocarya*

	PRESENT STUDY ¹					STACHURSKA					WODEHOUSE	
	\bar{x} (μ)	RANGE (μ)	\bar{x} (PORE NO.)	RANGE (PORE NO.)	% STEPH.	RANGE (μ)	MODAL CLASS	\bar{x} (PORE NO.)	RANGE (PORE NO.)	% STEPH.	SIZE (μ)	PORE NO.
§ CYCLOPTERA												
<i>paliurus</i>	30.1	25.9-33.1	4.1	3-5	100	24.5-40.3	30.0	4.1	3-5	100	33.1	5-7 ³
§ DIPTERA												
<i>fraxinifolia</i> ⁴	34.3	30.0-38.8	5.8	4-8	94.6	30.6-43.2	38.0	6.2	3-8	98	33-35	4-6
<i>hupehensis</i>	28.6	24.5-34.7	5.4	4-8	99.5	28.0-36.7	31.5	5.3	4-7	98	29-31	4-6
<i>stenoptera</i> ⁴	31.9	28.0-36.7	6.5	5-9	91.0	30.6-39.0	36.0	6.4	5-8	91	26-30	3-6
§ PLATYPTERA												
<i>delavayi</i>	32.2	28.6-38.8	5.8	4-7	85.6	— —	—	—	—	—	—	—
<i>forrestii</i>	—	— —	—	—	—	35.6-46.3	39.2	5.3	4-7	99		
<i>insignis</i>	35.5	32.6-38.8	5.3	4-7	98.8	33.8-43.5	38.6	6.3	5-8	100		
<i>rhoifolia</i>	33.4	30.6-36.7	6.5	5-8	80.8	37.8-46.8 ²	45.0 ²	7.6 ²	6-10 ²	25 ²		

¹ n = 50 for all collections² = values all unusual for *Pterocarya*, specimen probably a *Juglans*.³ = some heteropolar grains noted⁴ = two collections studied

TABLE 6. Pollen-Size and Pore-Number in Juglans

SPECIES	MEAN SIZE (μ)	SIZE RANGE (μ)	MEAN PORE NO.	PORE NO. RANGE	PERCENT STEPHANOPORATE
§ RHYSOCARYON					
<i>J. australis</i> *	32.3	28.6–36.7	10.9	7–17	< 1%
<i>J. boliviana</i>	30.3	25.9–34.6	10.0	8–12	
<i>J. californica</i> *	36.3	30.6–40.8	12.5	8–19	
<i>J. hirsuta</i> *	36.4	30.6–44.9	13.4	9–18	
<i>J. insularis</i>	32.1	28.6–34.7	9.9	8–14	
<i>J. jamaicensis</i>	32.0	28.8–36.0	9.7	6–12	< 1%
<i>J. major</i> **	34.7	24.5–40.8	11.5	4–17	
<i>J. microcarpa</i> *	34.8	30.6–40.8	13.8	9–22	
<i>J. neotropica</i> *	32.9	28.6–37.4	11.3	7–16	
<i>J. nigra</i> ***	34.7	28.6–40.8	17.4	9–37	
<i>J. olanchana</i>	32.4	28.6–34.6	11.4	8–14	
§ DIOSCARYON					
<i>J. regia</i> †	42.6	34.7–50.0	13.6	9–20	
§ CARDIOCARYON					
<i>J. sieboldiana</i>	37.4	32.6–42.8	8.3	6–11	3.3%
<i>J. cathayensis</i> *	33.8	30.6–40.8	7.3	5–10	ca. 1%
<i>J. cinerea</i> ††	35.6	28.6–40.8	7.8	2–15	10–35%
<i>J. mandshurica</i>	38.6	34.7–42.8	8.3	6–11	2.3%

* 2 collections

** 4 collections

*** size based on 3 collections, pore number on 42 coll. (Whitehead, 1963)

† 3 collections

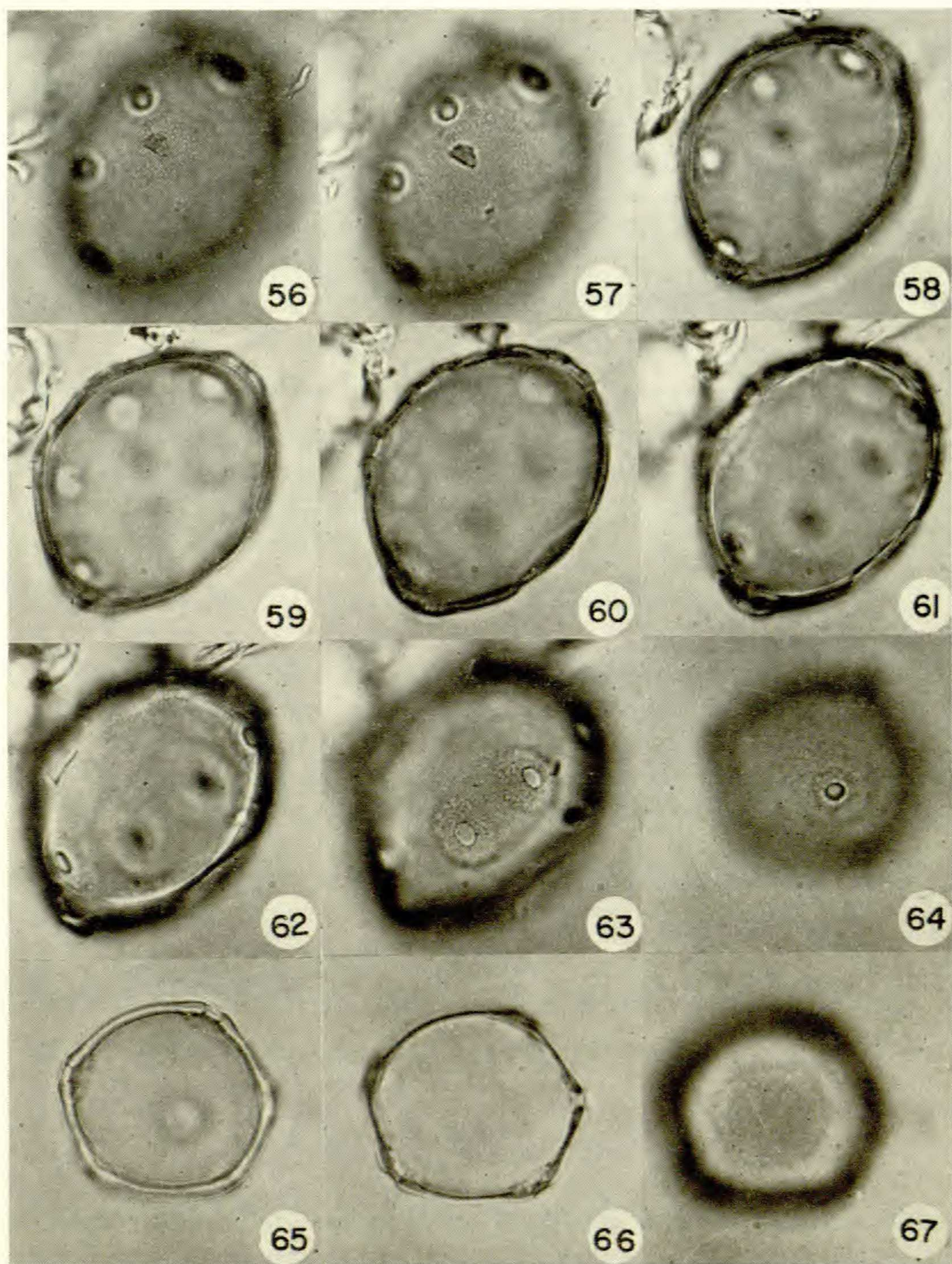
†† size based on 2 collections, pore no. on 44 coll. (Whitehead, 1963)

FIGURES 68–70). The frequency of stephanoporate grains is variable and is highest in one collection of *Juglans cinerea* (35%) (See TABLE 6 for further data). The grains are either circular or polygonal in polar view. Grain shape varies from suboblate to oblate-spheroidal. A distinct thinning of the ektexine occurs on the pore-free (proximal) pole (TEXT-FIGURES 58–62). The sculpture is distinctly scabrate.

The pores are generally aspidate, but the degree is highly variable (TEXT-FIGURES 69, 77). The vestibulum varies accordingly from a low, flattened cone to a fairly steep-sided one. The ektexine usually thickens slightly within the area of the vestibulum. In occasional grains the thickening is extremely pronounced (TEXT-FIGURE 71). The pore aperture ranges from circular to elongate in shape.

The pollen grains of *Juglans* vary in size from a minimum of 24.5 μ (one grain of *Juglans major*) to a maximum of 50.0 μ (one grain of *J. regia*). The species' means range from 30.3 μ for *J. boliviana* (1 collection) to 42.6 μ for *J. regia* (3 collections).

Individual collection data for pore number and pollen size are plotted in the scatter diagram (FIGURE 108).



TEXT-FIGURES 56-67. Magnification $690\times$. Each series (e.g., 56-63) represents successively lower levels of focus. 56-63, *Juglans regia*, equatorial view (note especially sculptural pattern and the polar thinning in 59-62). 64-67, *Juglans cathayensis*, polar view of hexaporate grain with one global pore.

The exine is of relatively uniform thickness over the entire grain surface except on the pore-free pole and within the vestibulum. The polar thinning appears to be similar to that observed in grains of *Carya*, and probably involves reduction of the columella layer. This has been corroborated by electron microscopy (Stone *et al.*, 1964). As the scabrate sculpture is

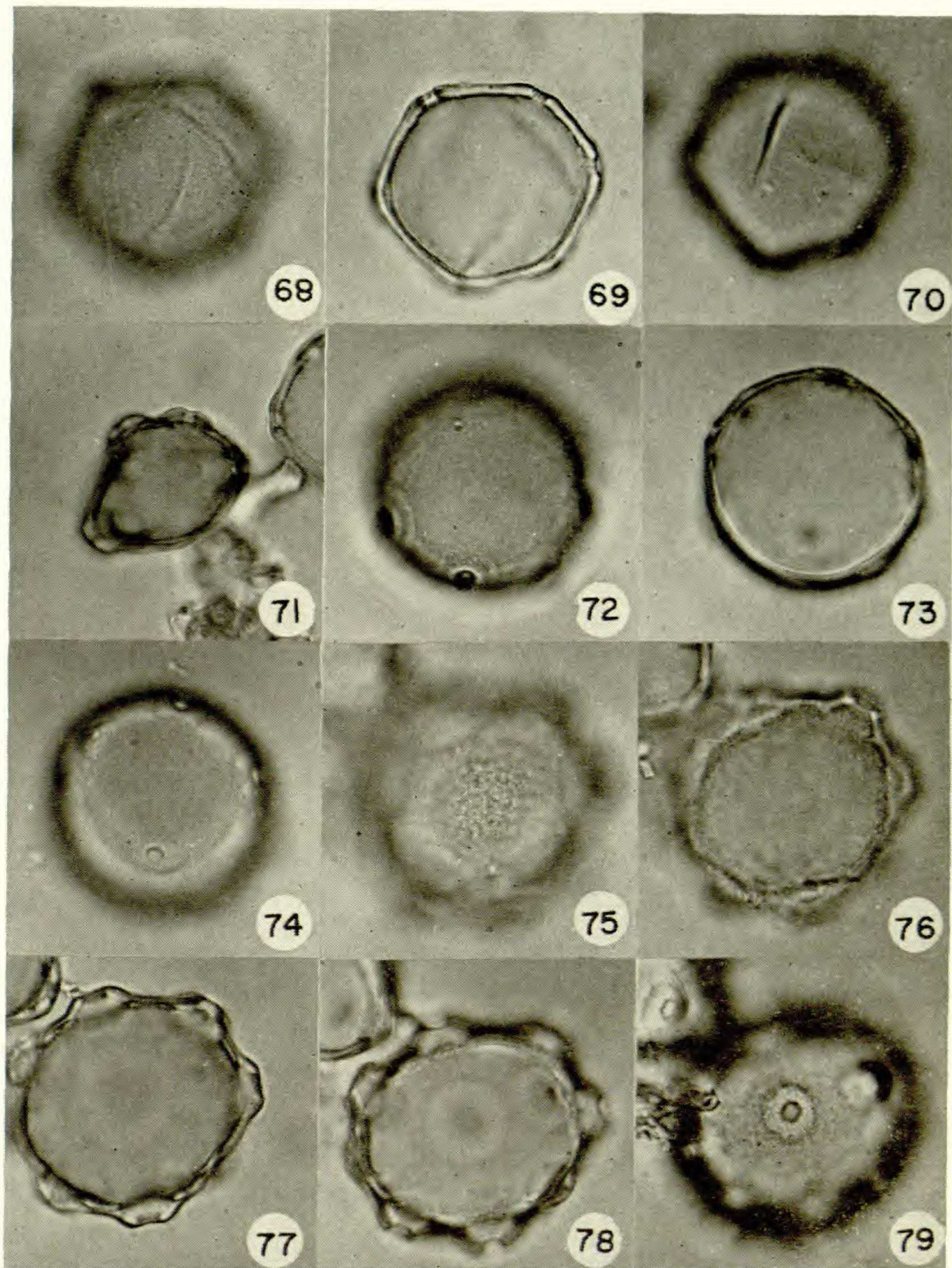
continuous over the thinning, at least some tectum must be present. The thinning is not detectable in stephanoporate grains. The exine appears to be relatively homogeneous. Columellae cannot be differentiated outside of the vestibular region and are often difficult to observe even within it. Once again, this observation appears to be based on an artifact of technique, since application of electron microscopy has shown that the columella layer occurs in all portions of the grain (Stone *et al.*, loc. cit.). The most usual situation is to find columellae concentrated at the base of the vestibulum (TEXT-FIGURE 107) and around the pore aperture. There is usually a columella-free zone of variable width between these two regions of concentration, although narrow "flames" of columellae may extend into it.

The sculptural pattern is continuous over the entire surface, including both vestibulum and proximal pole. It varies in distinctness from collection to collection, but is generally visible only under oil immersion. It appears to be most distinct in collections of *J. regia*, which also possess the largest grains.

Pollen size and pore number appear to have some taxonomic significance within the genus *Juglans*. This is clearly indicated on the scatter diagram (FIGURE 108). The species of section CARDIOCARYON are characterized by low pore number (means from 7.2 to 8.6 for individual collections), a higher frequency of stephanoporate grains (obviously correlated with pore number), and pollen grains ranging in size from approximately 33 to 39 micra. Pollen size is approximately the same for section RHYSOCARYON, but mean pore number is distinctly higher. It ranges from a minimum of 9.7 in *J. jamaicensis* to 17.4 in *J. nigra*. Pollen grains of *Juglans regia* (section DIOSCARYON) have approximately the same pore number as those of section RHYSOCARYON, but are distinctly larger. It would appear that grains of the *Cardiocaryon* type, which are similar to those of the less advanced genus *Pterocarya*, are primitive for the genus, and that the primary evolutionary trends have been towards an increase in pore number (culminating in *J. nigra*) and an increase in pollen size (leading to *J. regia*).

The markedly higher pore number characteristic of grains of *Juglans nigra* suggests that that species has occupied a position isolated (geographically and/or genetically) from other species of section RHYSOCARYON for some time. Similarly, the relatively small grain size and low pore number of the tropical American species of section RHYSOCARYON (*J. olanchana*, *J. australis*, *J. insularis*, *J. neotropica*, *J. boliviana*) suggests their early separation from other species of the section and retention of more "conservative" pollen morphological features.

The plotted points for the two collections of *J. microcarpa* pose a problem. One (*Palmer 11327*, from Texas) falls within the *J. nigra* region of the scatter diagram, while the other (*Greene, 1880*, from New Mexico) plots near the two New Mexico collections of *J. major*. It would be instructive to review the taxonomic status of the collections in question. For example, Manning (personal communication) has suggested that *J.*



TEXT-FIGURES 68-79. Magnification $690\times$. Each series (e.g., 68-70) represents successively lower levels of focus. 68-70, *Juglans cathayensis*, polar view of hexaporate grain with equatorial pores only. 71, *Juglans olanchana*, aberrant grain, note extraordinarily thick ectexine within the vestibulum. 72-74, *Juglans mandshurica*, polar view (note non-aspidate pores). 75-79, *Juglans major*, polar view of grain with abruptly aspidate pores.

microcarpa would not be expected to occur in the portion of New Mexico from which the collection derived; the specimen may represent *J. major* instead.

No other features appear to have taxonomic significance. The writer

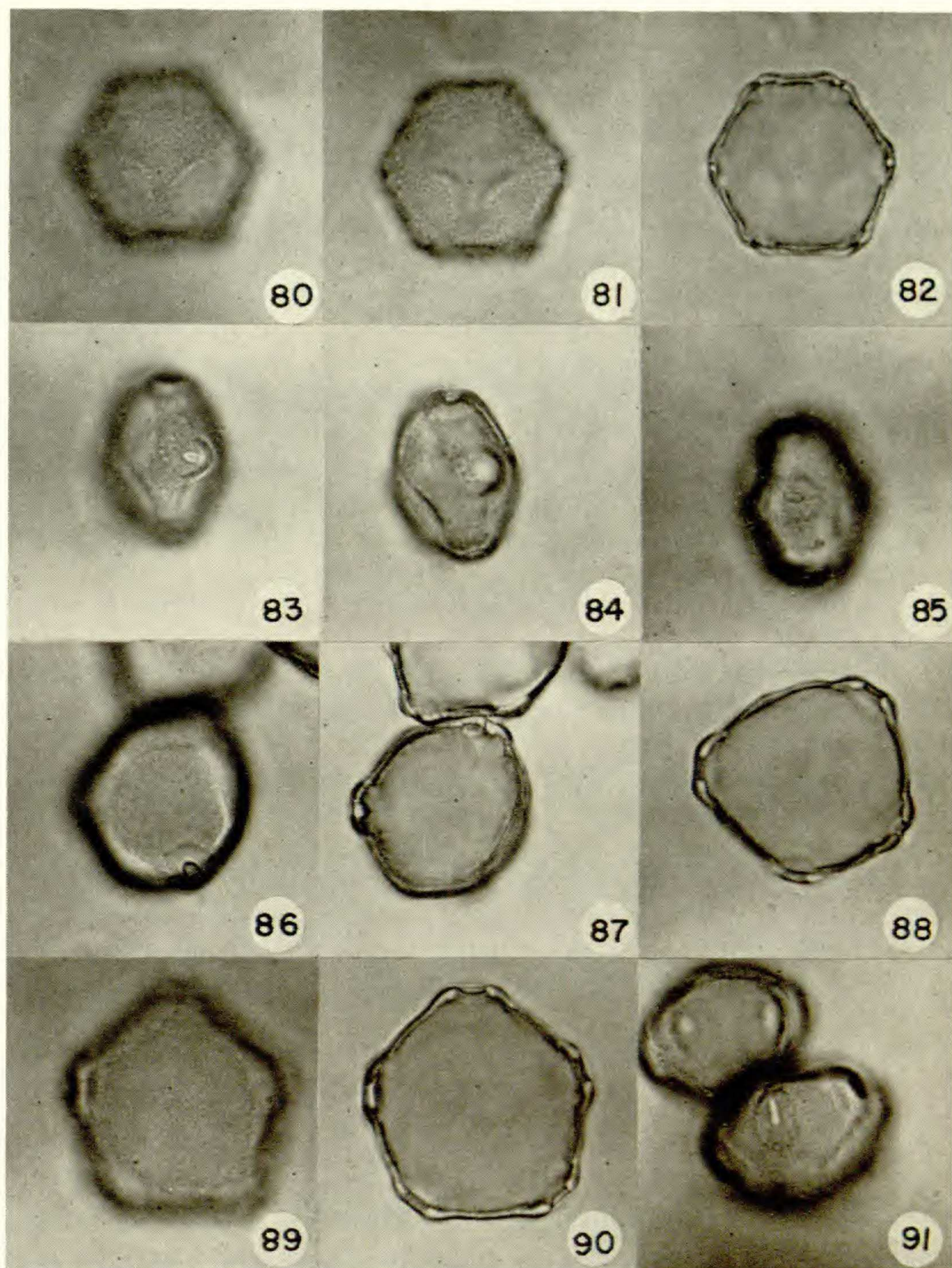
has not utilized the pollen groups established by Stachurska (1961) as, in general, they are based on characteristics (roundness of grains, protuberance of pores) that are apt to be profoundly altered by the state of preservation of the preparation; specifically the state of expansion of the grains. In fact, a number of Stachurska's photomicrographs (e.g., *Plate II*) are of grains which have been distended greatly by the swelling that one often encounters in glycerine-jelly preparations.

Following is a summary of observations on all *Juglans* collections studied.

Section RHYSOCARYON Dode. (1) *Juglans australis*: A few stephanoporate grains noted. This is highly unusual for the section. Distribution of columellae within vestibulum variable. (2) *J. boliviana*: distribution of columellae within vestibulum essentially "concentric," i.e., columellae concentrated around exopore and endopore, few between. (3) *J. californica*: "concentric" arrangement of columellae within vestibular area; a band of clumped columellae surrounding the pore aperture and another band at the base of the vestibulum. (4) *J. hirsuta*: columellae tightly packed within vestibulum, only a narrow, relatively columella-free zone between aperture and base of vestibulum. (5) *J. insularis* (*J. jamaicensis*): pore zone (vestibulum) relatively sharply defined; large and irregular patches of columellae at base of vestibulum and around the pore aperture; columellae widely spaced in between. (6) *J. major*: great variation from collection to collection. Both of the New Mexico collections have many grains with grossly protuberant pores and an extremely irregular scabrate sculpture. The other collections are more typical for the genus. Variation in fine structure is comparable; in some grains the pore zone is sharply defined by a definite concentration of columellae at the base of the vestibulum (FIGURE 107), in other grains there is a gradual transition from the homogeneous extra-vestibular exine to pore region. (7) *J. microcarpa*: considerable variation (see also previous discussion). Vestibulum structure as described for *J. californica*, with narrow columella-free zone between aperture and base. (8) *J. neotropica*: grains more rounded than in most collections, pores barely aspidate. Pore zone (vestibulum) relatively sharply defined; many large, irregularly distributed columellae within the zone. (9) *J. nigra*: vestibulum quite sharply defined; broad relatively columella-free zone extending from aperture nearly to base of vestibulum. Zone of columellae around pore aperture very narrow. Irregular "flames" of columellae extend from base of vestibulum into the columella-free area. (10) *J. olanchana*: many grains with unusually thick ektexine at the pore, great variability. Somewhat irregular distribution of columellae within the vestibular zone.

Section DIOSCARYON Dode. (1) *J. regia*: pore apertures appear to be unusually large. Sculpture often very distinct. A broad zone with large, irregularly spaced columellae around aperture; a rather diffuse zone of widely spaced columellae between this and the base of the vestibulum. Concentration of columellae also in basal zone.

Section CARDIOCARYON Dode. (1) *J. sieboldiana*: sharply defined pore



TEXT-FIGURES 80-91. Magnification $690\times$. Each series (e.g., 80-82) represents successively lower levels of focus. 80-82, *Pterocarya stenoptera*, polar view of hexaporate, stephanoporate grain. 83-85, *Pterocarya hupehensis*, equatorial view of hexaporate grain. 86, 87, *Pterocarya delavayi*, polar view of triporate grain. 88, *Pterocarya fraxinifolia*, polar view, tetraporate grain. 89, 90, *Pterocarya fraxinifolia*, polar view, pentaporate grain. 91, *Pterocarya stenoptera*, equatorial view, note elongate pore aperture.

zone; dense, narrow zone of columella at base; broad, columella-free zone extending from basal zone to relatively broad band of irregularly spaced columellae surrounding the aperture. Some irregular narrow rows of

columellae extending from base into columella-free zone. (2) *J. cathayensis*: sculpture very fine; fine structure variable; some grains with sharply defined pore zone, others not so. Some with broad columella-free zone within vestibulum, others with columellae relatively closely packed throughout vestibulum. (3) *J. cinerea*: pore zone not clearly differentiated; columellae relatively closely spaced. (4) *J. mandshurica*: grains quite rounded, pores barely aspidate. Pore zone not well differentiated. Broad zone of packed columellae around the aperture; occasionally a narrow columella-free zone between this and the region of densely packed columellae at the base of the vestibulum. Gradation from basal zone to dense ektexine of the grain surface.

DISCUSSION

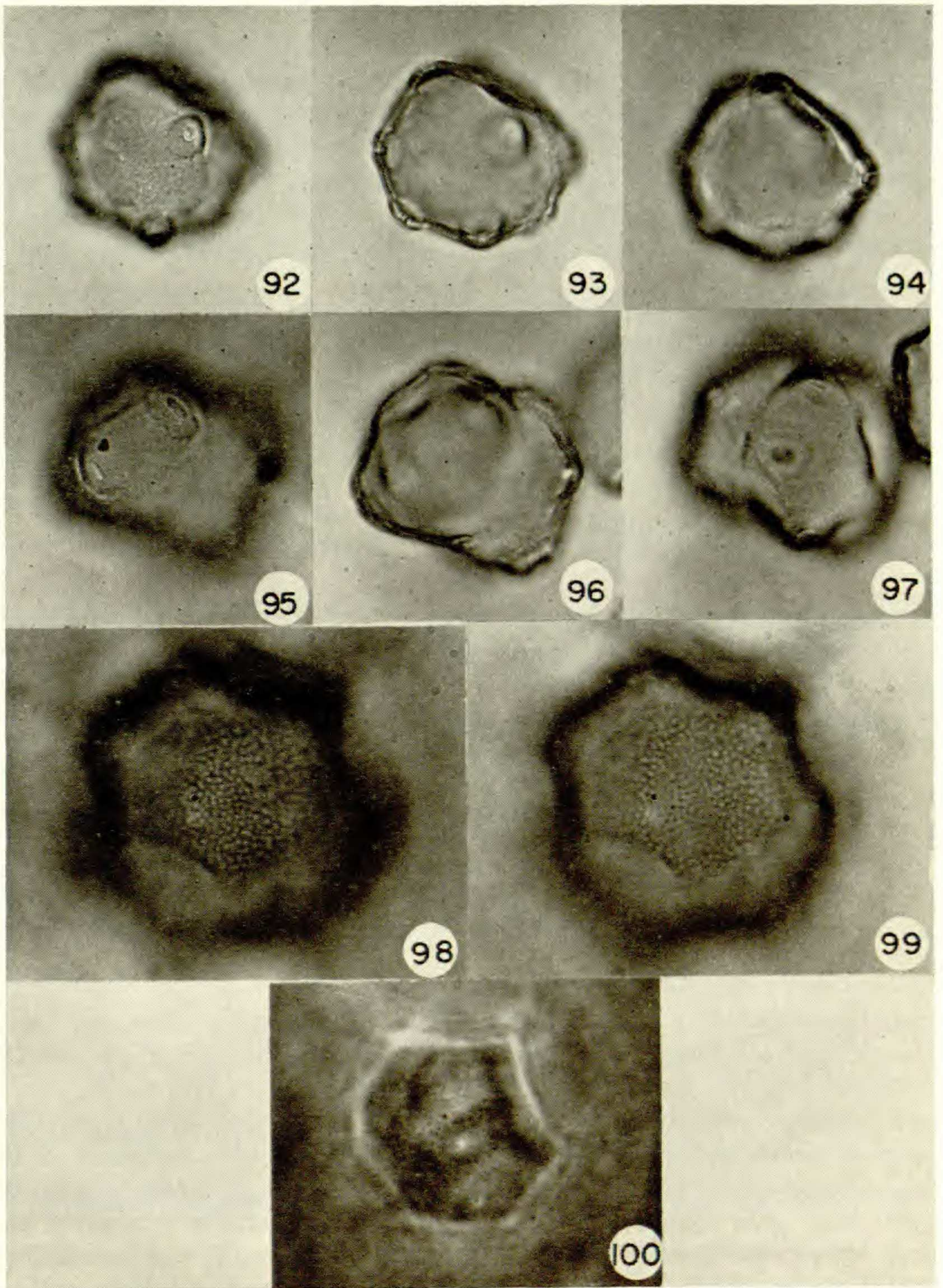
Generic distinctions. There are four different pollen types within the Juglandaceae: the triporate-isopolar *Engelhardia-Alfaroa* type; the triporate-pseudocolpate *Platycarya* type; the triporate-heteropolar *Carya* type; and the stephanoporate to periporate-heteropolar *Juglans-Pterocarya* type.

Pollen grains of the *Engelhardia-Alfaroa* type can be distinguished as follows: the pollen grains of *Platycarya*, although basically similar, always possess characteristic pseudocolpi. Grains of *Carya* are considerably larger (largest *Engelhardia-Alfaroa* grains: 26.2μ ; smallest *Carya* grains: 26.5μ) are always heteropolar and possess an ektexinous thinning on the proximal pole. Also, grains of *Carya* tend to be more circular in polar view and have much more distinctive columellae within the vestibular area. Pollen grains of the *Juglans-Pterocarya* type are larger, have a higher pore number, and tend to have more aspidate pores. Triporate-isopolar *Pterocarya* and *Juglans* grains do occur, but they tend to be larger and have more aspidate pores.

The pollen grains of *Platycarya strobilacea* can be distinguished easily from those of all other taxa in the family by virtue of the distinctive pseudocolpi. These are invariably present, even on tetra- and pentaporate grains.

The combination of three pores, heteropolarity, polar thinning, distinctive columellae and relatively large grain size serves to distinguish *Carya* grains from all other types. As mentioned above, the grains are invariably larger than those of the *Engelhardia-Alfaroa* type, are always heteropolar and possess the distinctive ektexinous thinning. The triporate *Juglans-Pterocarya* grains have equatorial, more aspidate pores, lack the localized polar thinning, and have a somewhat thinner exine. Furthermore, the columellae within the vestibular zone are not as large, distinct, or as irregularly distributed as in *Carya* grains. The diporate and tetra- to hexaporate grains of *Carya* are also easily recognizable.

Within the *Alfaroa-Engelhardia* group it would appear that a reliable generic distinction cannot be made on the basis of pollen morphology. However, it must be admitted that significantly more material of the two

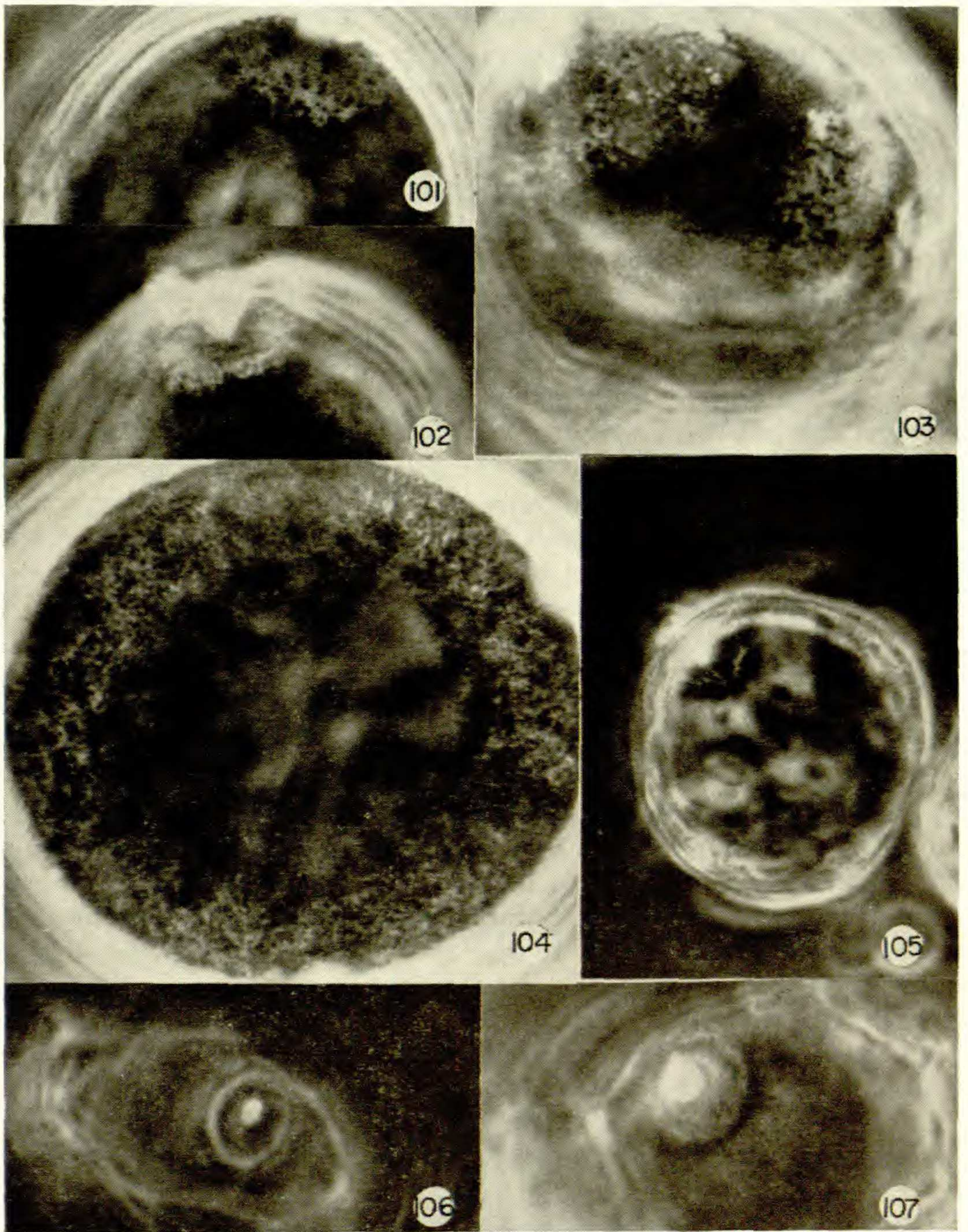


TEXT-FIGURES 92-100. Magnifications as noted. Each series (e.g., 92-94) represents successively lower levels of focus. 92-94, *Pterocarya delavayi*, polar view of heteropolar grain with seven pores, 690 \times . 95-97, *Pterocarya stenoptera*, fused grains, 690 \times . 98, 99, *Pterocarya stenoptera*, polar view, 1380 \times (note distinct scabrate sculpture). 100, same grain as in 98 and 99, phase contrast, 1380 \times .

genera must be studied before this possibility can be ruled out. On the basis of the material investigated, it is apparent that the grains of *Alfaroa* are distinguishable from at least one of the three *Engelhardia* pollen types (the *E. chrysolepis* type) and may be distinguishable from another (the *E. spicata* type). However, grains of *Alfaroa* and the *Engelhardia nudiflora* type appear to be indistinguishable. Pollen grains of the *E. chrysolepis* type are much smaller than those of *Alfaroa* (14.4 vs. 23.0 micra), are distinctly triangular (vs. rounded-triangular), are oblate (vs. sub-oblate), have an equatorially elongated endopore (vs. a circular one), the ektexine does not thicken within the vestibulum, and columellae cannot be differentiated (they are visible within the thickened ektexine of the vestibulum in *Alfaroa* grains). The distinctions between *Alfaroa* grains and those of the *E. spicata* type are by no means so certain, partly because it is not clear whether the *E. spicata* type represents a distinct "species" or rather an anomalous variant of the *E. nudiflora* type. Grains of the *E. spicata* type tend to be more spheroidal, the vestibulum is often less distinct, and the exine is often sharply undulating, perhaps due to an unevenly thickened ektexine.

The grains of *Juglans* and *Pterocarya* are very similar. The variational extremes appear to be relatively distinct (e.g., tetra- and pentaporate, stephanoporate grains of *Pterocarya* and periporate, heteropolar grains of *Juglans* (§ RHYSOCARYON and § DIOSCARYON). However, as is evident from the scatter diagram, the photomicrographs, and the data presented in TABLES 5, 6, and 7, there is a variational continuum from *Pterocarya* to *Juglans* section CARDIOCARYON. Pore number, grain size, and frequency of heteropolar grains tend to be higher in section CARDIOCARYON, but there is overlap for all of these characteristics. Pollen size cannot be used because there is a general correlation between pollen size and pore number; those grains of *Juglans* (§ CARDIOCARYON) with the lowest pore number are also smallest. Furthermore, the heteropolar tendency is detectable in many stephanoporate *Pterocarya* grains in that one pore is apt to be positioned slightly off of the equator and the grains are often somewhat plano-convex in equatorial view. Other morphological criteria are equally difficult to apply. The pore aperture in *Pterocarya* is apt to be elongated meridionally, but this is by no means constant. *Pterocarya* grains are generally more oblate in shape, but this characteristic is associated with pore number and degree of heteropolarity; heteropolar grains are more spheroidal (and stephanoporate-isopolar *Juglans* grains are more oblate than heteropolar ones). The polar ektexinous thinning is not a definitive characteristic, because it is not present in stephanoporate *Juglans* grains, and is extremely difficult to detect (and possibly absent) in many heteropolar grains with relatively low pore number. There are no apparent differences in columella distribution.

Grains with from 6 to 8 pores are extremely difficult to identify with certainty. However, certain suggestions can be made on the basis of the data presented in TABLE 7 and FIGURE 109. It can be seen that five- and six-pored grains are much more frequently encountered in *Pterocarya*,



TEXT-FIGURES 101-107. Phase contrast photomicrographs. Magnification $1420 \times$. 101, *Carya sinensis*, pore area (note restricted vestibulum, sharp vestibular boundary, widely scattered columellae within vestibulum). 102, *Carya tonkinensis*, pore area (note restricted vestibulum, sharp boundary). 103, *Carya cordiformis*, equatorial view, ekstexinous thickening extensive, reaching far beyond vestibulum. 104, *Carya tomentosa*, polar view, columellae evident throughout equatorial region, including interporium. 105, *Engelhardia parvifolia*, polar view (note presence of columellae along "ridges" on grain surface). 106, *Pterocarya delavayi*, equatorial view of pore, note vestibulum relatively free of columellae. 107, *Juglans major*, pore area (note "concentric" arrangement of columellae within vestibulum, here concentrated around endopore).

that seven-pored grains are met with frequently in both taxa, and that eight- and nine-pored grains are much more common in members of *Juglans* section CARDIOCARYON. Furthermore, there is an obvious difference between taxa within each pore-number class, since the frequency of stephanoporate grains is consistently higher in *Pterocarya*. For example, 97 per cent of hexaporate *Pterocarya* grains are stephanoporate, and only 44 per cent of *Juglans* (§ CARDIOCARYON) grains; and 71 per cent of seven-pored *Pterocarya* grains are stephanoporate, 4 per cent of *Juglans*.

Such data are instructive, but must be handled with extreme caution, since a number of assumptions are involved. First, when dealing with fossil material, it would be necessary to assume that the populations of *Juglans* and *Pterocarya* which contributed pollen to the depositional basin in question possessed pore-number and heteropolar-frequency characteristics comparable to those determined in the present study. Secondly, since relatively few collections were studied, there is no guarantee that the data are representative for the two taxa. Furthermore, it is quite possible that significant interspecific and intraspecific differences in populations may exist for both characteristics (this could apply to both modern and fossil material). This possibility can be visualized from the histograms for extreme individual collections which are also presented in TEXT-FIGURE 2. (This should not be construed as proof of the existence of such differences in populations, merely as a hypothetical example.) If, for example, the populations of *Juglans* and *Pterocarya* growing in the vicinity of a depositional basin possessed frequency characteristics similar to those of the individual collections of *Juglans cinerea* and *Pterocarya rhoifolia*, separation of grains would be virtually impossible. On the other hand, the presence of populations with characteristics approximating those for *Juglans sieboldiana* and *Pterocarya insignis* would make discrimination considerably easier. A further complication is that the distributions (for pore number and frequency of heteropolar grains) determined in the present study may be derived, the result of a long evolutionary sequence. It seems probable that within the *Juglans-Pterocarya* complex small pollen size, low pore number and low frequency of heteropolar grains are primitive characteristics. Hence one would expect *Juglans* section CARDIOCARYON grains from the early Tertiary to have characteristics more closely approximating those of modern *Pterocarya* species. Similarly, one might expect lower pore number within the early Tertiary species of *Pterocarya*.

It must be concluded that individual *Pterocarya-Juglans* section CARDIOCARYON grains will pose a difficult problem. If such grains are sufficiently common, it would be instructive to prepare a statistical analysis of pollen size, pore number, and frequency of heteropolar grains. This would allow more reasonable suggestions as to the taxa involved and provide a more meaningful basis for the delimitation of form genera and form species.

Subgeneric categories. The degree to which subgeneric identifications can be made is suggested by the following key to generalized pollen types. It should be emphasized that specific identifications are not im-

TABLE 7. Pore-number and heteropolar grain frequency in Juglans § Cardiocaryon and Pterocarya

PORE-NUMBER	JUGLANS § CARDIOCARYON *									PTEROCARYA **												
	<i>sieboldiana</i>	<i>cathayensis</i>	<i>cathayensis</i>	<i>mandshurica</i>	<i>cinerea</i>	<i>cinerea</i>	TOTALS	%	% STEPH. (OF CLASS)	<i>paliurus</i>	<i>rhoifolia</i>	<i>rhoifolia</i>	<i>fraxinifolia</i>	<i>fraxinifolia</i>	<i>insignis</i>	<i>delavayi</i>	<i>hupehensis</i>	<i>stenoptera</i>	<i>stenoptera</i>	TOTALS	%	% STEPH. (OF CLASS)
3						1 ¹	1 ¹	0.4	100	2										2	0.4	100
4							0	0.0	(100)	39			1		1	2	1			44	8.8	100
5			1 ¹		1 ¹	1 ¹	3 ³	1.2	100	9	8	1	32	3	33	16	30	6	3	141	28.2	100
6	2 ²	3 ¹	11	1 ¹	4 ⁴	2 ²	23 ¹⁰	9.2	43.5		25	13	17 ²	34	15	23 ³	18	27	22	194 ⁵	38.8	97.4
7	8	20	21	9	12 ³	10	80 ³	32.0	3.8		14 ¹⁴	32		11 ¹	1 ¹	9 ⁹	1 ¹	12	20 ³	100 ²⁰	20.0	71.0
8	20	22	11	22	6	7	88	35.2	0.0		3 ³	4 ²		2 ²				4	5 ⁵	18 ¹²	3.6	33.0
9	13	4	5	12	2	3	39	15.6	0.0									1 ¹		1 ¹	0.2	0.0
10	6	1	1	5		1	14	5.6	0.0											500 ¹⁷		
11	1			1			2	0.8	0.0													
							250 ¹⁷															

* exponent indicates number of stephanoporate grains

** exponent indicates number of heteropolar grains

plied; each pollen type may include a number of different species. In some cases only the variational extremes can be separated from closely related types. As the range of variation has been considered in preparing the key, many taxa may be keyed out at several points (e.g., *Pterocarya* under triporate, stephanoporate, and periporate-heteropolar). The size criteria apply *only* to modern material prepared as outlined previously and mounted in silicone oil. Correction factors must be employed for fossil material and modern grains prepared by different techniques. The pollen-shape classes can be used only for fully expanded grains that have not been compressed either by fossilization or pressure from the coverslip.

1. Grains triporate (occasionally diporate).
 2. Grains isopolar.
 3. Pseudocolpi present. *Platycarya* type.
 3. Pseudocolpi absent.
 4. Grains $> 26\mu$; pores aspidate, columellae within slightly thickened ekstexine of vestibulum clear, often concentrated around exopore and endopore. *Pterocarya-Juglans* § *Cardiocaryon* type.
 4. Grains $< 26\mu$; pores very slightly to not at all aspidate; columellae not visible, or visible and tightly packed within vestibulum.
 5. Grains $12-17\mu$; triangular; oblate; exopore meridionally elongated; endopore equatorially elongated; columellae not visible. *Engelhardia chrysolepis* type.
 5. Grains $17-26\mu$; rounded-triangular to circular; suboblate to oblate-spheroidal; exopore and endopore more or less circular; columellae visible within vestibulum.
 6. Exine of uniform thickness, grain outline smooth. *Engelhardia nudiflora-Alfaroa* type.
 6. Exine unevenly thickened, grain with undulating outline. *Engelhardia spicata* type.
 2. Grains heteropolar (pores positioned off of the equator toward one pole, ekstexinous thinning of pore-free (proximal) pole).
 7. Grains $< 33\mu$; relatively isopolar; vestibulum and ekstexinous thickening restricted; sharp line of demarcation between vestibulum and exine of polar hemisphere. *Carya tonkinensis-sinensis* type.
 7. Grains $> 33\mu$; strongly heteropolar; vestibulum and ekstexinous thickening less restricted; demarcation between vestibulum and polar region apt to be gradational. *Carya* type.
1. Grains with more than 3 pores.
 8. Grains stephanoporate (isopolar); 4-7 pores.
 9. Pseudocolpi present. *Platycarya* type.
 9. Pseudocolpi absent.
 10. Grains $> 26\mu$; pores aspidate; columellae within vestibulum clear, often concentrated around exopore and endopore; grains angular in outline. *Pterocarya-Juglans* § *Cardiocaryon* type.
 10. Grains $< 26\mu$; pores slightly to not at all aspidate; columellae not visible, or visible within vestibulum (and there tightly packed); outline angular or rounded angular.
 11. Grains $12-17\mu$; angular (square, pentagonal); oblate; exopore meridionally elongated, endopore equatorially elongated; columellae not visible. *Engelhardia chrysolepis* type.

11. Grains 17–26 μ ; rounded angular to circular; suboblate to oblate-spheroidal; exopore and endopore more or less circular; columellae visible within vestibulum.
 12. Exine of uniform thickness, grain outline smooth.
 *Engelhardia nudiflora-Alfaroa* type.
 12. Exine unevenly thickened; grains with undulating outline.
 *Engelhardia spicata* type.
8. Grains heteropolar.
 13. Pores positioned off of the equator towards one pole, but none global (hence grains not periporate-heteropolar); pores not strongly aspidate; wall relatively thick. *Carya* type.
 13. Grains periporate-heteropolar (possessing at least one global pore); pores often strongly aspidate; wall comparatively thin.
 14. Pores 9 or fewer. *Pterocarya-Juglans* § *Cardiocaryon* type.
 (Grains less than 30 μ are more apt to be *Pterocarya*).
 14. Pores more than 9.
 15. Pores more than 19. *Juglans nigra* type.
 15. Pores less than 19.
 16. Grains more than 40 μ *Juglans regia* type.
 16. Grains less than 40 μ . . . *Juglans* § *Rhysocaryon* type.

When one disregards the variational extremes for all taxa and considers only the most frequently occurring values for both quantitative and qualitative characteristics, it is clear that a more precise subdivision of some of the pollen types is possible. While little can be done with *Engelhardia-Alfaroa* and *Platycarya* poses no problem, more precise assignments can be made within the *Juglans-Pterocarya* complex. Pollen morphology could also be of considerable use within *Carya*, but is more difficult to employ.

The following suggestions can be made with respect to the *Juglans-Pterocarya* complex. Stephanoporate grains (3–7 pores) are most probably those of *Pterocarya*; especially those that are less than 32 μ in size. Periporate-heteropolar grains with low pore number (6–9) are apt to be from *Juglans* section CARDIOCARYON (generally 33–39 μ in size). Periporate-heteropolar grains with from 9 to 13 pores and of relatively small size (30–35 μ) may belong to the tropical American complex (*J. australis*, *J. boliviana*, *J. insularis*, *J. neotropica*, and *J. olanchana*). Somewhat larger grains (33–39 μ) with from 9 to 16 pores can be assigned to *Juglans* section RHYSOCARYON. Grains with more than 16 pores are those of *Juglans nigra* (size: 33–36 μ). Grains larger than 39 μ with from 11 to 15 pores are those of *Juglans regia*.

In addition, a few generalizations can be made concerning *Carya* pollen. First, it is obvious that there is a correlation between pollen size and ploidal level (Stone, 1961, 1963; Whitehead, 1963). In general the smallest grains occur in the diploids of section APOCARYA, the largest in the tetraploids of section CARYA. There are obvious exceptions. For example, *Carya illinoensis* (2n) of section APOCARYA has rather large grains (mean = 46.1 μ) and *Carya floridana* (4n) of section CARYA has rather

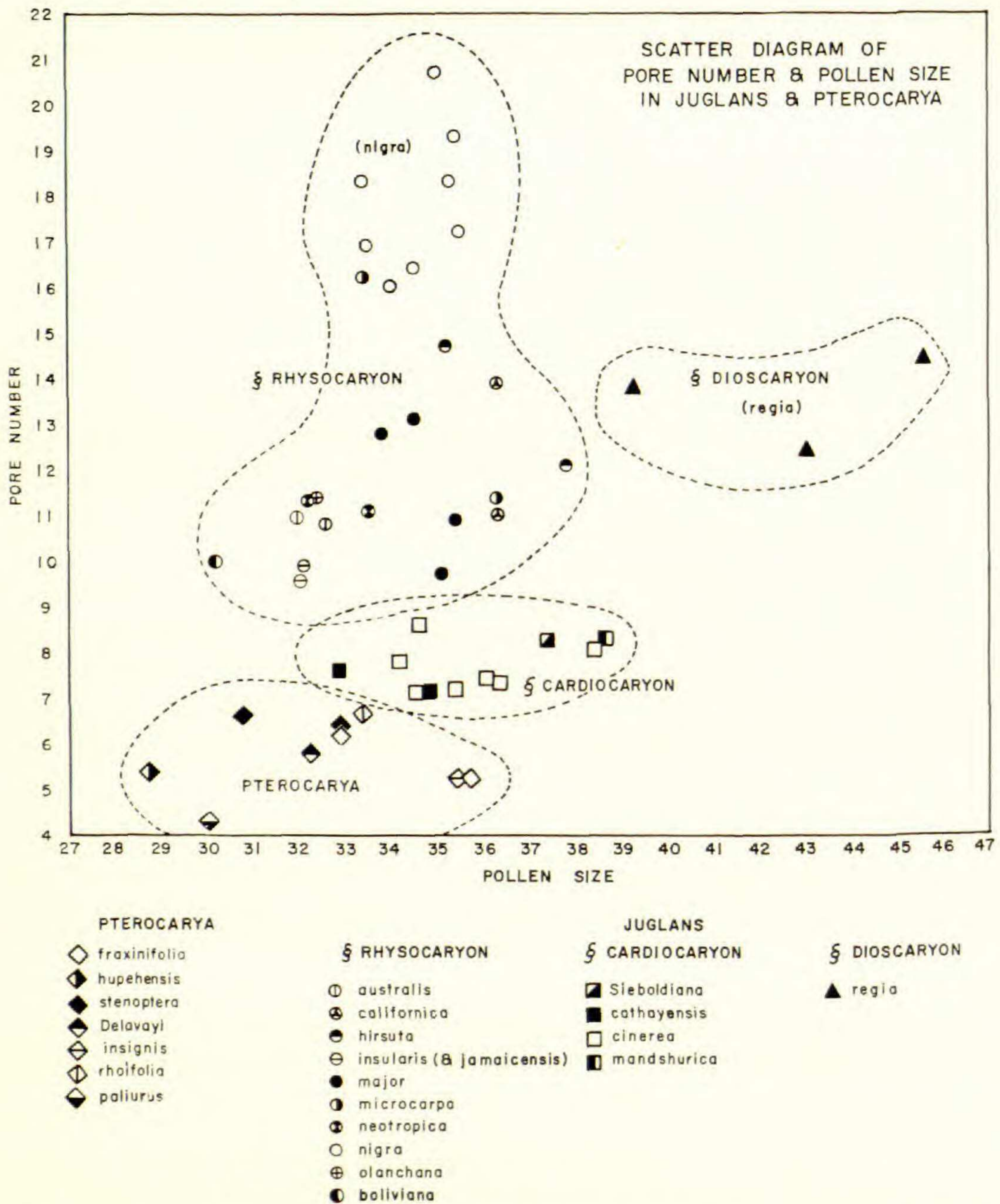


FIGURE 108. Scatter diagram of pore-number and pollen-size in *Juglans* and *Pterocarya*.

small pollen (reported by Stone (1963)) to be 44.1μ . This latter mean is from fresh grains mounted in cotton-blue-lactophenol. By applying a correction factor of -1.03 , it can be suggested that it would correspond to 42.8μ for grains treated as in the present study. Small grains are also found in *Carya sinensis* of section RHAMPHOCARYA.

Relatively isopolar grains have been observed in *Carya tonkinensis*, and *Carya illinoensis* and in *C. sinensis*. As is mentioned previously, this is a difficult criterion to employ, since it can be influenced profoundly by the state of compression of the grains.

Some species possess grains with a sharply defined and somewhat re-

stricted vestibular area. In such grains there is an abrupt change from the homogeneous exine of the general grain surface (within which columellae are not detectable) to the vestibular zone, within which columellae are distinct and irregular in size, shape, and distribution. The condition is most prevalent in a few species of section APOCARYA (*C. aquatica* (one collection does not show it), *C. illinoensis*, and *C. tonkinensis*). It has also been found in *Carya texana* (§ CARYA) and *C. sinensis*. The vestibular zone is also sharply defined in *Carya cordiformis* (§ APOCARYA), but in that species the ekstexinous thickening (the zone within which the columellae can be recognized) is extraordinarily extensive, encroaching upon both interpore area and pole.

In a few species there was a rather distinctive thickening of the ekstexine within the vestibulum. This was found in both collections of *Carya*

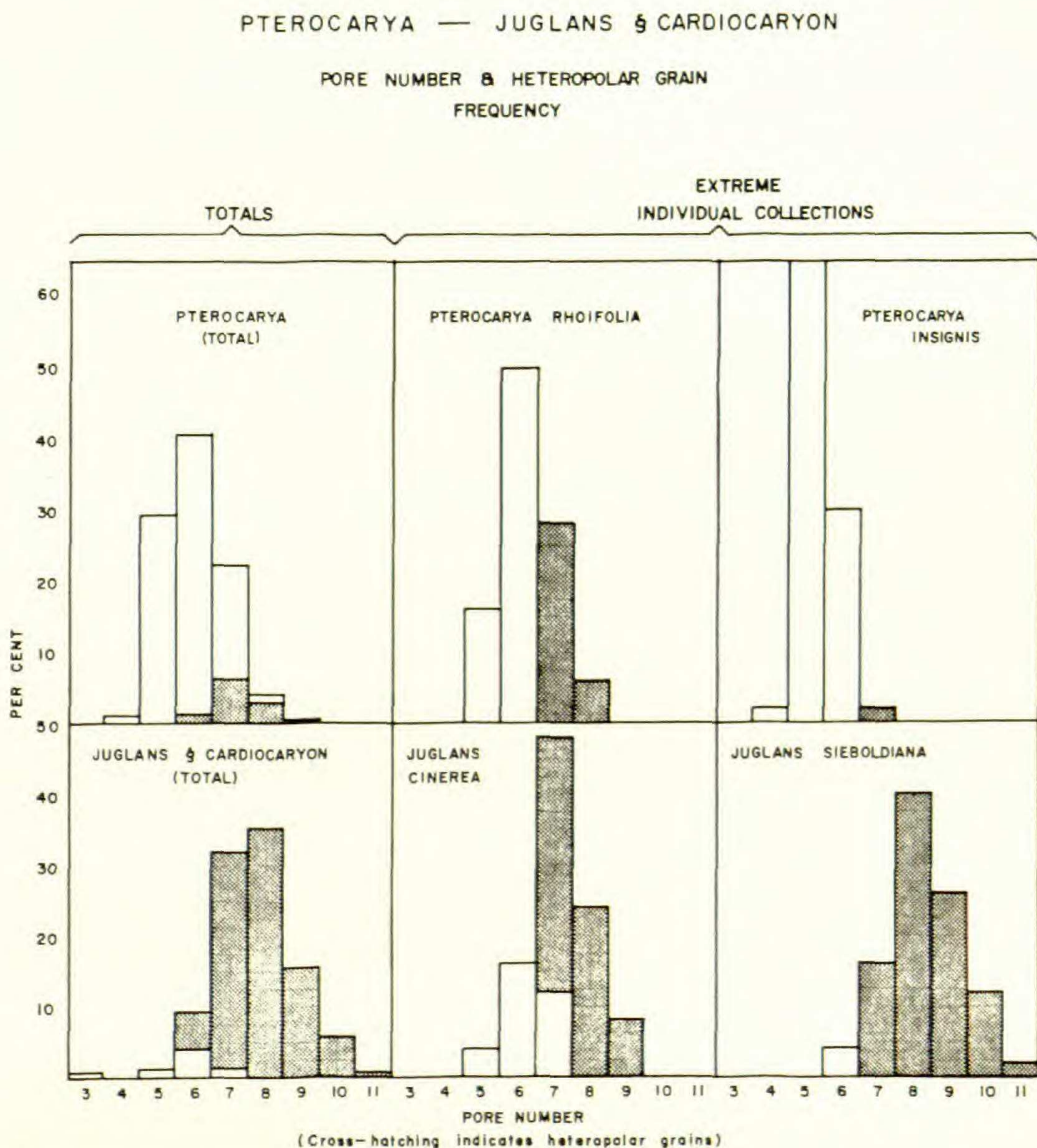


FIGURE 109. *Pterocarya-Juglans* § *Cardiocaryon*: pore-number and heteropolar grain frequency.

illinoensis and the single collection of *Carya pallida* (§ CARYA). It has also been reported for the latter species by Stachurska (1961).

The pollen grains of *Juglans regia* and *Carya illinoensis* are of further interest because of their relatively large size. The mean for *Juglans regia* (43μ) is considerably larger than that for other species of the genus (means usually $32-36\mu$) and the grains of *C. illinoensis* (mean = 46μ) are much larger than those of other species of section APOCARYA and as large as those of the tetraploids of section CARYA. Stone (1963) has also noted this for *C. illinoensis*, and has suggested that large grain size might be correlated with increased fertility, as is the case in other taxa. It is significant that both of these species have had a long history of cultivation; hence the recent evolutionary trends within the species may be largely controlled by the selective pressures imposed by man. Certainly increased fertility would be selected for, and if pollen grain size were correlated, as seems likely, it is reasonable to suggest that the evolution of larger pollen in these taxa has been a relatively recent phenomenon, stimulated and directed by man's practices.

Phylogenetic considerations. Pollen morphology supports the indications from floral morphology (Manning, 1938, 1940, 1948) and wood anatomy (Heimsch & Wetmore, 1939) as to relationships of genera. The correlated evidence from these previous studies indicates that the *Engelhardia-Alfaroa* complex (see also Manning, 1949) is primitive and that the *Juglans* and *Carya* lines are relatively advanced. *Pterocarya* appears to occupy an intermediate position, relatively close to *Juglans*. *Platycarya* presents some interesting problems, being advanced with respect to wood anatomy (Heimsch & Wetmore, loc. cit.) and primitive with respect to type and bearing of inflorescence (Manning, 1938).

When speculating on the evolution of pollen types within the family, it would be reasonable to look for the most primitive grains within the *Engelhardia-Alfaroa* group and the most advanced in *Juglans* and *Carya* (and *Platycarya*?). The grains of the *Engelhardia-Alfaroa* are small, pre-vaillingly triporate, and isopolar; those of *Juglans* and *Carya* larger, heteropolar, possess an ektexinous thinning on the proximal pole, and, in the case of *Juglans*, have a higher pore number. It would thus appear that the primary evolutionary trends have involved an increase in pore number, grain size, and heteropolarity. To some extent these trends have been independent of one another. The general trends are indicated in FIGURE 110.

Within *Engelhardia* and *Alfaroa* there are at least two pollen types represented: first, the very small, triangular, oblate *E. chrysolepis* type, secondly, the larger, more spheroidal *E. nudiflora-Alfaroa* type. The *E. spicata* type is problematical, and may be nothing more than an aberrant variant of the basic *E. nudiflora* type. For the moment it will be disregarded. On the basis of wood anatomy (Heimsch & Wetmore, 1939) and floral morphology (Manning, 1938, 1949) *Alfaroa* appears to be the most primitive member of the family. It would then be logical to suggest that

POLLEN MORPHOLOGICAL RELATIONSHIPS
WITHIN THE JUGLANDACEAE

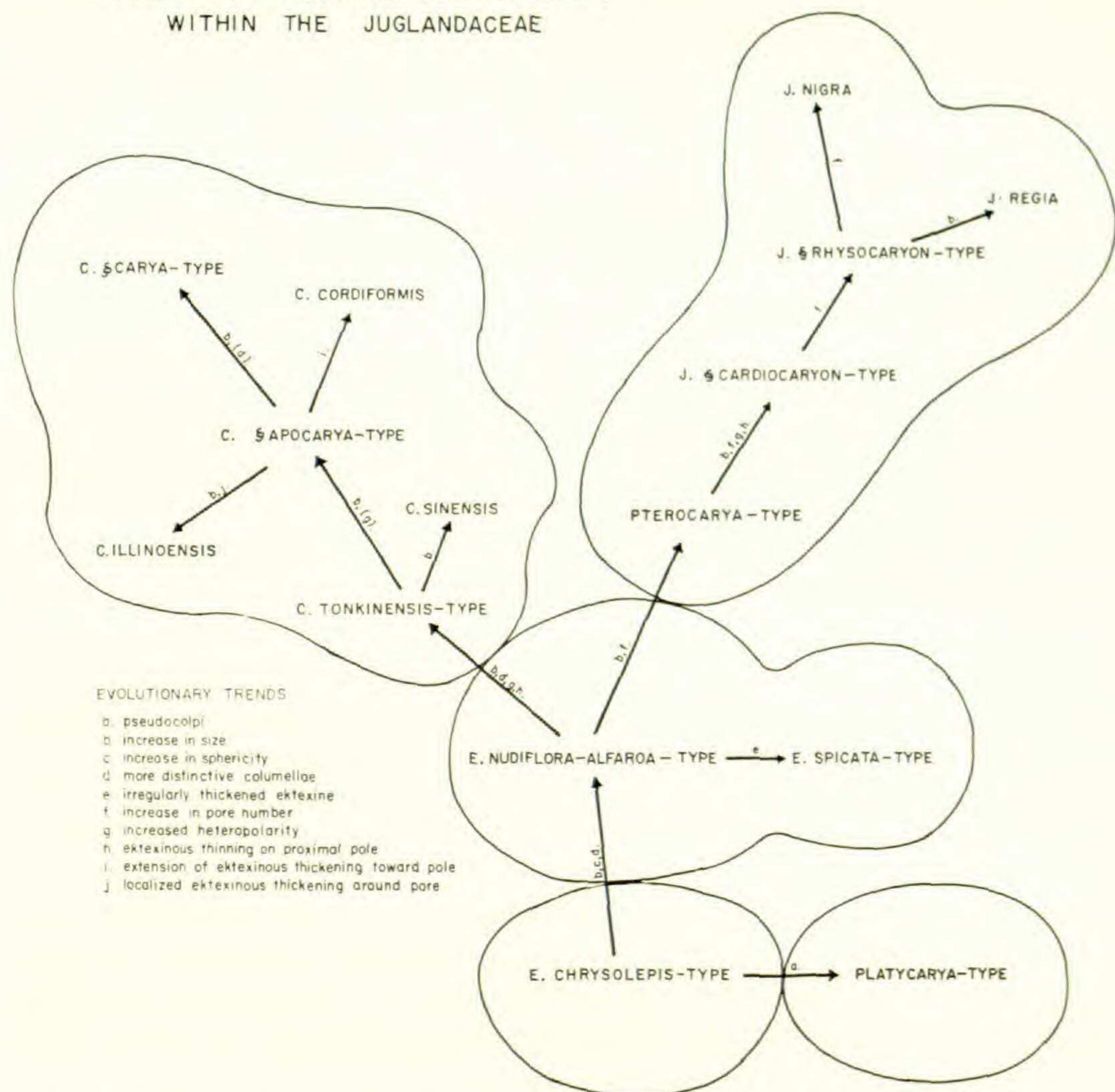


FIGURE 110. Pollen morphological relationships within the Juglandaceae.

pollen grains of the *E. nudiflora-Alfaroa* type, found also in this genus, are the most primitive, and that the *E. chrysolepis* type has been derived through a reduction in pollen size, increasing angularity, and reduction of columellae. However, there are several arguments against this view. First the general trend within the family appears to have been an increase in grain size and an increase in the distinctiveness of columellae. The evolution of the *E. chrysolepis* type from the *E. nudiflora-Alfaroa* type would require a reversal of this. Secondly, the remarkable similarity of *Platycarya* and *E. chrysolepis* type pollen may be of significance. Should *Platycarya* grains lack pseudocolpi, they would be virtually indistinguishable from those of the *E. chrysolepis* type. Both grains are extremely small, triangular, oblate, have a meridionally elongated exopore and an equatorially elongated endopore, and a homogeneous exine (it does not thicken within the vestibulum and no columellae can be differentiated). The scabrate sculpture of both types is extremely fine (a function of grain size) and uniform. All these features suggest that the *Platycarya* type has evolved from the *E. chrysolepis* type through the development of localized

arcuate thinnings of the ektexine (reduction of columella layer and inner tectum). Should this suggestion be valid, then it is more logical to assume that the *E. chrysolepis* type is primitive, and that the *Platycarya* and *E. nudiflora-Alfaroa* types are evolved (also the *E. spicata* type). In this context, it is perhaps significant that both *Platycarya* and *Engelhardia chrysolepis* possess inflorescence types (terminally placed androgynous panicles) which Manning (1938) considers to be the most primitive for the family.

From the triporate-isopolar base there were apparently two primary evolutionary lines, one involving increase in grain size and heteropolarity (culminating in the grains of *Carya* section CARYA), the other, involving increase in pore number, increase in grain size, and heteropolarity, leading through *Pterocarya* and culminating in *Juglans nigra* (high pore number) and *Juglans regia* (large pollen grains).

It is difficult to ascribe evolutionary significance to the pollen morphological characteristics observed within the genus *Carya*, since the features are subtle and display great variation. However, it is probable that the most primitive grains would be those most closely approximating the *Engelhardia-Alfaroa* type, i.e., small size, relative isopolarity, restricted ektexinous thickening and vestibulum. Such grains are found in various species of section APOCARYA and also in *Carya sinensis* (§ RHAMPHOCARYA). The grains of *Carya tonkinensis* and *C. sinensis* are more similar to those of *Engelhardia-Alfaroa* than those of other species, hence may represent the most primitive type. This situation is not unexpected, since preliminary evidence indicates that species of section APOCARYA are primitive (Stone, 1962) and that *Carya tonkinensis* may be the most primitive. Wood of this species is less distinctly ring porous and possesses more heterogeneous rays than that of other species (Heimsch & Wetmore, 1939). More recently (Leroy, 1953) it has been shown that the wood of *Carya sinensis* is virtually indistinguishable from that of *C. tonkinensis*.

The larger, more heteropolar grains of section CARYA, especially those of the tetraploids, can be considered more advanced. The recognizable variants of the APOCARYA type (e.g., *C. cordiformis* and *C. illinoensis*) are doubtless short side lines.

The last pollen type to be considered is that found in *Juglans* and *Pterocarya*. Following the evolutionary sequence suggested for the family as a whole it seems probable that the relatively small stephanoporate grains of *Pterocarya* are more primitive than those of *Juglans*. This is in harmony with the intermediate position suggested by morphological and anatomical studies (Heimsch & Wetmore, 1939; Manning, 1938).

Since there appears to be a continuum between *Pterocarya* and *Juglans*, it is interesting to speculate on the relationship of these genera. On the basis of pollen morphology alone the relationship would appear to be close. This is also suggested by wood anatomy (Heimsch & Wetmore, 1939) and floral morphology (Manning, 1938, 1940, 1948). The present study indicates that the relationship is closest between species of the section CARDIOCARYON and *Pterocarya* (see, for example, the scatter diagram).

This alliance is also supported by the evidence from wood anatomy and floral morphology. Heimsch and Wetmore (loc. cit.) have noted that species of *Cardiocaryon* have vascular elements with thinner walls than those of other species in the genus as a whole. This condition is similar to that prevailing in *Pterocarya*. Furthermore, species of section CARDIOCARYON differ from the rest of the genus in possessing more flowers (12–20) per pistillate catkin (Manning, 1938) and fewer stamens (7–18) per staminate flower (Manning, 1948). In both of these characteristics the section CARDIOCARYON resembles *Pterocarya*. In addition, there is a similarity between the two taxa in the number of bracts, bracteoles, and sepals in both staminate and pistillate flowers (Manning, 1940, 1948). Thus evidence from a variety of lines suggests a close relationship between *Juglans* and *Pterocarya* and most particularly between *Juglans* section CARDIOCARYON and *Pterocarya*.

Following this line of reasoning, it is suggested that the scatter diagram (FIGURE 108) depicts the evolutionary trends within the *Juglans-Pterocarya* complex. The base of the sequence is occupied by the "Pterocaryoid" grain of relatively small size, low pore number, and high frequency of isopolarity. The "Cardiocaryoid" type can be derived from this by an increase in pollen size, pore number and heteropolarity. The evolution of the "Rhysocaryoid" type of grain from the latter simply involves an increase in pore number. From the "Rhysocaryoid" type there were apparently two independent evolutionary lines, the first involving an increase in pore number and culminating in *Juglans nigra*, the second involving a stabilization of pore number and an increase in pollen size (culminating in *Juglans regia* (§ DIOSCARYON)). The relatively isolated position occupied by the tropical American species of section RHYSOCARYON (*J. olanchana*, *J. neotropica*, *J. insularis*, *J. australis*) might suggest an early time of isolation from the main RHYSOCARYON line, and the retention of relatively "primitive" characteristics (low pore number and small pollen size).

The evolutionary trends outlined here are summarized graphically in FIGURE 110. This is designed only to portray the evolution of pollen types, not necessarily the relationships of extant taxa. The two may well be parallel (as seems to be the case within the *Juglans-Pterocarya* complex), but obviously such phylogenetic speculations must involve a consideration of all data bearing upon the problem.

SPECIMENS EXAMINED²

1. *Alfaroa costaricensis* Standley var. *costaricensis*. COSTA RICA: *Skutch* 4684 (A).
2. *Alfaroa costaricensis* Standley var. *elongata* Manning. COSTA RICA: *Skutch* 4685 (A).

² Material studied was obtained from the herbarium of the Arnold Arboretum (A), the Gray Herbarium (GH), the Botanical Museum, Copenhagen (C), the U.S. National Herbarium (US), the herbarium of Bucknell University (BU), and the Instituto Interamericano de Ciencias Agrícolas (IICA). DGU numbers refer to slides in the reference collection of the Geological Survey of Denmark.

3. *Alfaroa manningii* León. COSTA RICA: *León* 3331 (BU).
4. *Engelhardia apoensis* Elmer ex Nagel. BORNEO: *Kostermans* 7417 (US).
5. *Engelhardia nudiflora* Hook. f. MALAYA: *Haniff*, 1928 (C; DGU — 2865).
6. *Engelhardia parvifolia* C. DC. PHILIPPINES: *Ramos & Edaño* 28761 (A).
7. *Engelhardia serrata* Bl. var. *cambodica* Manning. CHINA: *Henry* 11774 (A).
8. *Engelhardia spicata* Bl. INDIA: *Hooker & Thomson*, no date (C; DGU — 3916).
9. *Engelhardia spicata* Bl. var. *acerifolia* (Reinw.) Koorders & Valetton. CHINA: *Ko* 55858 (A).
10. *Engelhardia spicata* Bl. var. *colebrookiana* (Lindl. ex Wall.) K. & V. INDIA: *Abraham* 87? (C; DGU — 3910).
11. *Engelhardia chrysolepis* Hance (= *E. roxburghiana* Wall.). CHINA: *Steward & Cheo* 584 (A); *Ching* 1980 (A). VIETNAM: *Collector unknown* (C; DGU — 2915).
12. *Engelhardia pterocarpa* (Oerst.) Standl. COSTA RICA: *León* 1819 (IICA).
13. *Platycarya strobilacea* Sieb. & Zucc. JAPAN: *Uno*, 1952 (A). KOREA: *Tacquet* 3113 (A).
14. *Carya glabra* (Mill.) Sweet. (Specimens cited in: Whitehead, 1963).
15. *Carya laciniosa* (Michx. f.) Loud. (Specimens cited in: Whitehead, 1963).
16. *Carya leioderms* Sarg. (Specimens cited in: Whitehead, 1963).
17. *Carya ovalis* (Wang.) Sarg. (Specimens cited in: Whitehead, 1963).
18. *Carya ovata* (Mill.) K. Koch. (Specimens cited in: Whitehead, 1963).
19. *Carya pallida* (Ashe) Engl. & Graebn. (Specimens cited in: Whitehead, 1963).
20. *Carya texana* Buckl. (Specimens cited in: Whitehead, 1963).
21. *Carya texana* Buckl. var. *arkansana* Sarg. (Specimens cited in: Whitehead, 1963).
22. *Carya tomentosa* Nutt. (Specimens cited in: Whitehead, 1963).
23. *Carya tomentosa* Nutt. var. *subcoriacea* Sarg. (Specimens cited in: Whitehead, 1963).
24. *Carya aquatica* Nutt. (Specimens cited in: Whitehead, 1963).
25. *Carya cordiformis* (Wang.) K. Koch. (Specimens cited in: Whitehead, 1963).
26. *Carya cordiformis* (Wang.) K. Koch. var. *latifolia* Sarg. (Specimens cited in: Whitehead, 1963).
27. *Carya illinoensis* (Wang.) K. Koch. (Specimens cited in: Whitehead, 1963).
28. *Carya myristiciformis* (Michx. f.) Nutt. (Specimens cited in: Whitehead, 1963).
29. *Carya tonkinensis* Lecomte. CHINA: *Tsai* 53190 (A).
30. *Carya sinensis* Dode. INDOCHINA: *Pételot* 6376 (A).
31. *Pterocarya paliurus* Batalin. CHINA: *Wilson* 901 (A).
32. *Pterocarya fraxinifolia* (Lam.) Spach. PERSIA: *Sintenis* 1348b (A). Locality unknown: *E. Koehne*, no date (C; DGU — 3936).
33. *Pterocarya hupehensis* Skan. CHINA: *Wilson* 404 (A).
34. *Pterocarya stenoptera* C. DC. CHINA: *Sun* 1091 (A); *Handel-Mazzetti* 11580 (C; DGU — 3941).
35. *Pterocarya delavayi* Franchet. CHINA: *Ching* 20475 (A).
36. *Pterocarya insignis* Rehd. & Wils. CHINA: *Schneider* 930 (A).
37. *Pterocarya rhoifolia* Sieb. & Zucc. JAPAN: *Tschonoski* 1864 (GH); *Faurie*, 1904 (A).
38. *Juglans australis* Griseb. ARGENTINA: *Peirano* 18700 (GH); *Schreiter* 1045 (BU).

39. *Juglans boliviana* (C. DC.) Dode. PERU: *Knowles*, 1956 (BU).
40. *Juglans californica* S. Wats. U.S.A.: *Clokey & Templeton* 4465 (GH); *Parish* 6908 (A).
41. *Juglans hirsuta* Manning. MEXICO: *Pringle*, 1906 (GH); *Mueller & Mueller* 428 (A).
42. *Juglans insularis* Griseb. CUBA: *Rehder* 1157 (A).
43. *Juglans jamaicensis* C. DC. CUBA: (cultivated) *Walsingham*, 1948 (BU).
44. *Juglans major* (Torr.) Heller. U.S.A.: *Gillespie* 5665 (GH). *Lowell*, 1911 (A); *Eastwood* 8387 (A); *Skehan* 29 (A).
45. *Juglans microcarpa* Berl. U.S.A.: *Palmer* 11327 (A); *Greene*, 1880 (A).
46. *Juglans neotropica* Diels. ECUADOR: *Rose* 22807 (GH). PERU: *Vargas* 7409 (BU).
47. *Juglans nigra* L. (Specimens for pore number study cited in: *Whitehead*, 1963). U.S.A.: *Biltmore Herbarium* 1314 (A); *Thomas* 2148a (A); *Drushel*, no date (C; DGU — 3928).
48. *Juglans olanchana* Standley & Williams. SAN SALVADOR: *Calderon* 1528 (GH).
49. *Juglans regia* L. CHINA: *Steward & Cheo* 86 (A); *Simeon* 334 (A); *Chiao*, 1926 (C; DGU — 3865).
50. *Juglans sieboldiana* Maxim. JAPAN: *Funu Agric. Coll.*, 1885 (A).
51. *Juglans cathayensis* Dode. CHINA: *Wilson* 371a (A); *Yü* 411 (A).
52. *Juglans cinerea* L. (Specimens for pore number study cited in: *Whitehead*, 1963). U.S.A.: *Deane*, 1886 (GH); *Williams*, 1897 (GH).
53. *Juglans mandshurica* Maxim. MANCHURIA: *Komarov* 463 (A).

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LETTERS FROM CHARLES SPRAGUE SARGENT TO
REGINALD SOMERS COCKS, 1908-1926 *

Edited by JOSEPH EWAN

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March 26, 1920.

Please collect for us as many specimens as you can of the Azaleas which have passed as *nudiflora*. Apparently this species does not get into Louisiana at all. The specimens which we collected at Winnfield April 6, 1913, Palmer's 8882 and 9462 from Natchitoches, one specimen which we collected April 12, 1915, at Lakes Charles and one which I collected in 1885 at Pineville belong to *Azalea canescens*. There appears to be a distinct form of this last in Mississippi, Louisiana and Texas differing in the glabrous under surface of the leaves and more slender corollas. This is Palmer's Natchitoches specimen 7228 and the plant with white flowers which we collected at Lake Charles April 2, 1913. So far as we know now this form always has white flowers, or nearly white flowers, and grows in swamps or on the borders of swamps.

The specimens which I have enumerated are the only ones we have from Louisiana. I suspect that this new form, which will probably have to be treated as a variety of *canescens*, grows in eastern Louisiana as it seems to be common and the only form in southern Mississippi. We have specimens, however, of no early-flowering *Azalea* from eastern Louisiana. Please look out for this this spring as we are working here on a monograph of American species. The only *Azalea* from eastern Louisiana which we have is what has passed for *Azalea viscosa*. It is not that species which does not get south at all, but Small's *Azalea serrulata* which grows from central Florida through southern Mississippi to eastern Louisiana.

I wonder if we are going to live long enough to get the trees and shrubs from Louisiana properly straightened out. I hope you will do what you can in this *Azalea* business this spring and send us as much material from as many localities as possible.

240

April 8, 1920.

I read in a Boston paper that Louisiana is to be hunted from end to end for a mysterious species of *Aronia* and for an Ash-tree, and that the New Orleans Garden Club has been called on by Harvard to perform this service, so I suppose great results can be expected. In the meantime I wish you would dry for me flowers of as many of the different *Azaleas* cultivated in the old Louisiana gardens as you can reach. We are making here a

* Continued from volume 46, p. 361.

systematic study of the Azaleas of eastern Asia which have been in a helpless state of confusion, especially cultivated plants, and we are interested to know if possible which were the Azaleas cultivated in the southern states.

On the Butler place I made a couple of specimens which turned out to be *Azalea ledifolia* but there are probably other species cultivated. From the specimens we shall be able to name the species at least to which the plants belong. I should think that this would be a subject in which the members of your Garden Club would be interested; still if they want to hunt swamps for a missing Ash-tree I would not discourage them.

241

April 16, 1920.

I have this morning your letter of April 12th. Do not forget that *Crataegus silvicola* Beadle grows in eastern Louisiana. Unfortunately I have had to change the name of *drimophila* because there is an older *Crataegus silvicola* published in Europe.

It is much more than two years since I have heard from your lady friend in Crowley.²¹ She did send me some May Haws but I can hardly believe that I told her the May Haw had practically disappeared from western Louisiana where it seems to be more abundant than anywhere else.

Is there any reason why Azaleas should not grow in New Orleans gardens? They certainly do well in West Feliciana Parish, at the Butler place and at Natchez. We are taking a good deal of interest in these plants now and are beginning to print a book about all the Azaleas in the world. I should like to send you some plants in the autumn for your friends if there is a chance of their doing well in Louisiana. Azaleas would certainly do well, I should say, in the Selma region.

We are still having very bad weather and although the frost is all out of the ground spring is not making much headway. I noticed this morning that the buds of *Dirca palustris* were just beginning to open.

Hope to hear from you soon.

242

May 27, 1920.

The evergreen plant of which you send me a fragment is *Cocculus laurifolius*²² from southern China. The package with *Azaleas*, etc., was duly received. These appear to be all *Rhododendron canescens* but you will know more about them later. Rehder's present theory is that *nudiflorum* is not a southern plant at all.

I am horrified at what you write about *Adelia* fifty feet high and a tree. If your plant is really a tree how can it be kept out of my Manual? I have seen thousands of these *Adelias* in different parts of the country and growing under favorable conditions. They were never trees in the true sense of the word, that is with a single trunk, but really large shrubs.

²¹ Presumably PHEBE SUSAN LOVELL.

²² Introduced sometime after 1898 by Ida Richardson.

Please write me at once about your Baton Rouge specimen. If it is a tree what is the diameter of the trunk, and especially how tall is it before it begins to divide into branches? I hate the idea of putting *Adelia* in the Manual, but after the big specimens of *Styrax* we saw in West Feliciana Parish there is no knowing what may happen in western Louisiana. If *Adelia* is to be put in the Manual I ought to know about it at once.

I had yesterday a very pleasant visit from your friend Miss King who talked to me a great deal about you and your success with your Garden Club and with the ladies of New Orleans generally. She was here only a short time and I was able to show her very little of the Arboretum which she seemed to enjoy. She agreed with me that you ought not to delay much longer the publication of your Flora. You of course cannot begin to print it until you have been here for consultation with various books, specimens, etc. There is no better time for you to do this work than this summer. I expect to be here all summer and to be living alone most of the time, so come and stay with me as soon as you like and work here and in Cambridge. Do not think about this but come.

243

June 11, 1920.

I have yours of the 5th of June and read with regret what you say about the *Adelia*. How tall was the trunk with a diameter of eighteen inches, that is how soon did it begin to branch above the surface of the ground? Perhaps you can get some further information about the size of the plant on the Alabama River. I really don't want to put this plant in the new Manual but I am afraid you will compel me to do so. I will write you about your Huckleberry as soon as the specimens are mounted.

Your specimens of *Aronia* which you send me have leaves as large or perhaps even larger than the type of Hooker's variety *macrophylla*, so I suppose if you want to include this variety in your Flora you have authority to do it.

Please reconsider your assumed inability to come north this summer. You have to publish your Flora sometime and even if you should put off doing so for another fifty years it would not be complete when it was published. I do not believe it is wise to wait any longer, and you certainly cannot publish until you have come north to see various books. There is no time so good as this summer for doing this, and I think if you only stayed three or four weeks and worked hard you would do everything there was to be done here. At this end of the route there is every reason why you should come this summer and not put it off longer. It will be an awful pity if all the work you have done on the Louisiana flora was wasted, and it will be if your book is not published. Delays are fatal.

244

June 21, 1920.

I have a bundle with two specimens of *Azalea* and a *Prunus*. I understand that the *Prunus* is the plant from which you sent, in a pasteboard

box, a small quantity of fruit a few days ago. Am I right in this supposition? I do not know this Plum at all but I trust you haven't found a new species. The leaves look a good deal like those of *P. angustifolia* variety *varians* but the fruit, judging by the stone, can be no form of *angustifolia*. I should take the fruit for that of *munsoniana* which, however, does not ripen before the middle of August. As I understand it *angustifolia* ripens in Alabama by the 1st of May and the fruit of this new plant does not ripen much before the middle of June and much earlier than *munsoniana* which also grows in the Selma region.

We have in the herbarium here your Nos. vii. 1913; 15 and 16 of 1914, and 896 of 1914. These are placed under *P. munsoniana*. Do any of these numbers belong to the new tree and, if not, have you flowers to accompany the leaves and fruit sent this year? We have also Nos. 1 and 3, March 1914 which are probably *P. munsoniana*. As I understand the new tree does not sucker. Is it common and how large does it grow? I cannot bear the thought of another Plum tree.

Please answer this letter by return mail and tell me everything you know about "*Prunus Cocksii*," of which I hope there is but a single plant, in which case I won't feel like doing anything about it.

245

August 3, 1920.

I am struggling to arrange the *Prunus* material in this herbarium and to write up the genus for the Manual. The only thing I have really accomplished is to convince myself that I know nothing whatever about American Plum-trees. I have, however, made the following notes for you.

Alabama. Yellow fruit, August 20, 1918, is probably *P. umbellata*. Your leaf specimen sent in October of that year is very poor. Please press and send us others as soon as possible. Notice that the leaves are much more pubescent than those of the ordinary form of *P. umbellata*. This has always made me hesitate about this specimen.

Prunus, June 15, 1920, I suppose we must call *angustifolia varians* until we know something more about it. Please send us more herbarium material with well grown leaves. If this determination is correct the plants must be an escape from cultivation. I do not understand your fruit "in long racemes." *Prunus* never has racemose fruit.

Pine Flat near creek, No. 892. We have fruit but do not find leaf specimens. Please send these if you can find the tree.

You do not appear to have collected *Prunus americana* in the Selma district although Harbison found it there and we have several specimens from him.

Eastern Louisiana. The following I refer to *Prunus lanata*. 1 and 2, Butler Plantation, March 28, 1910. 20, West Feliciana, October 1914. Covington, March 28, 1911. Open woods, Hammond, May 13, 1910. Laurel Hill, Nos. 2 and 3, October 7, 1910. Ventries Plantation, April 27, 1910, *Prunus* No. 2, Butler Plantation, "Clover Hill, 200 feet west of pond," March 28.

Western Louisiana. *Lanata*, Palmer, Nos. 7015, 80677[sic], 7069, 8859, 7074, 7051, 8742, 7008, 8789.

To *Prunus mexicana* I refer Laurel Hill No. 4, October 7, 1910; Pineville, Cocks, September 20, 1912, a tree fifteen miles west of Opelousas, C. S. S., October 10, 1913; Ruston, Cocks, No. 6, August 24, 1914; Archibald, Cocks, No. 18, October 1910; Alto, Cocks, No. 14, October 1910. We have Cocks' numbers 1 and 2 Vinton, April 3, 1912, flowers only. Can you complete these?

The specimen we collected on the Gentilly Road below New Orleans April 15, 1915, seems to be *Prunus americana*, the only specimen of this species which I have seen from Louisiana. This should be followed up and mature leaves and fruit collected.

Does not *Prunus caroliniana* grow in western Louisiana? It does in eastern Louisiana and is very common indeed in eastern Texas. We have nothing here, however, to show that it grows in western Louisiana. Our only specimen from Louisiana is from West Feliciana. I should suppose that it would grow in the neighborhood of Hammond and in other places nearer the coast. I should like to know about this.

Cocks's No. 7, Sardis, received July 19, 1913, with large slightly pubescent leaves which might be those of *P. americana*, and small globose fruit. If this fruit and leaves belong to the same plant I do not know it. Can you do anything about this?

No. 9, Sardis, July 1913. I have placed this with *P. lanata*. Harbison's No. 101, Selma, September 20, 1919, is the same. I enclose a leaf of your No. 9. Your No. 9 and Harbison's No. 101 are the only specimens of this species from Alabama which I have seen and they probably represent its most eastern range. I hope you will investigate your No. 9 further and get more material. I should like to know if it is common in the region.

246

August 7, 1920.

I find in the Gray Herbarium a specimen of *Prunus caroliniana* collected by Drummond in New Orleans which of course may mean Covington. There is also a Hale's specimen in the Gray Herbarium without locality, and a specimen from Ocean Springs, Mississippi, collected by Tracy.

247

September 7, 1920.

Dr. Robert Ridgway, the distinguished ornithologist, has established a sort of bird haven on a piece of land with an area of eighteen acres near Olney, Illinois. He claims that there are sixty-four native trees growing on these eighteen acres. This of course is a very large number, but I should not be surprised if there were even more species growing, perhaps not on eighteen acres but within a radius of eight or ten miles of Selma. Can you make out a list of the Selma trees? It would be interesting to publish this in connection with Dr. Ridgway's list.

If you are in North Carolina I am sure you are enjoying yourself there. As I do not know your address I am sending this to New Orleans in the hope that it will reach you sooner or later.

248

Sept. 27, 1920.

I find no specimen of *Zanthoxylum clava-herculis* from eastern Louisiana in this herbarium. I suppose it grows there and that you have a specimen for us.

249

November 2, 1920.

There are two or three very fine Formosa conifers which we can send to you if you can find some one in New Orleans to take care of them. As they grow at a considerable altitude in Formosa there is a chance that they may prove hardy in Louisiana. Among them will be the *Taiwania* which is one of the great trees of the world. We can send you a few young plants of the Ogechee Lime, *Nyssa Ogechee*, which I do not suppose any one has cultivated before. It is worth growing for the beauty of the fruit. Also a Formosa oak.

I do not know what sort of a permit will be needed in order to send these plants into Louisiana. If one is needed will you get it from the proper authorities and send it to me? As these are all tender plants they ought to be started from here before it gets too cold.

250

November 4, 1920.

Do you remember the Persimmon trees which we saw on the Moon Plantation in Richland Parish? Some of the trees were growing in water and others on dry land. These trees had broad often cordate leaves very pubescent on the lower surface. You sent fruit of these but we foolishly allowed it to dry instead of putting it in formalin and it is not possible now to form an idea of the shape. Do you remember if it was broader than high and flattened at the ends? We have a specimen of Persimmon collected by you in swamps near New Orleans with cordate leaves pubescent below. Would it be possible to get some fruits from a tree growing in the New Orleans swamps? I am anxious to see the size and shape of the swamp Persimmon which seems to me to represent a pretty distinct variety of *Diospyros virginiana*. It is possible that the fruit is still on the trees; if not, it is perhaps on the ground underneath them. I find, with the exception of this from New Orleans, we have no Persimmon specimen from eastern Louisiana.

251

November 10, 1920.

We have no specimen of *Euonymus atropurpureus* from Alabama or Louisiana. I should suspect, however, that it would grow in Dallas County,